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# Benthic Studies in Buzzards Bay. I. Animal-Sediment Relationships[1]

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ABSTRACT

During October and November 1955 a bottom faunal study was undertaken at 19 localities in Buzzards Bay, Massachusetts. The number of animals ranged from 1,064 to 12,576/m² with a mean number of 4,430. In comparison with certain other areas these numbers appeared small and seemed to be due to the relatively low concentrations of chemical nutrients and modest primary production of the region. Two faunal assemblages were recognized: one, present in the muddy sediments and dominated by the lamellibranch *Nucula proxima* and the polychaete *Nephthys incisa* was essentially the same community described from Long Island Sound; the other, restricted to the sandier sediments and characterized by species of the amphipod genus *Ampelisca*. The two primary feeding types, the filter-feeders and the deposit-feeders, numerically dominated in the sand and mud sediments, respectively. The distribution of certain dominant deposit-feeders in Long Island Sound and Buzzards Bay was poorly correlated with the silt-clay fraction of the sediment. However, when clay alone was used, a much better agreement was obtained. It was suggested that clay is probably the most valid criterion for the distribution of deposit-feeders. The distribution of infaunal filter-feeders seemed related to the degree of sorting and the median grain size of the sediment, with largest populations present in well-sorted fine sand. The hydrodynamic implications of this distribution are discussed.

## INTRODUCTION

A quantitative benthic survey was undertaken in Buzzards Bay, Massachusetts, during October and November of 1955. Four survey stations (Fig. 1: H, J, P, and R) were selected as being representative of different widespread sediment and faunal assemblages. They were subjected to intensive monthly sampling over a twelve-month period (February 1956–February 1957) with the purposes of measuring some of the dynamic properties of benthic communities such as growth, mortality, and organic turnover of the more important species components; of obtaining additional data on animal-sediment relationships; and of defining the niches of the numerically abundant species. This paper is concerned with animal-sediment relationships.

Buzzards Bay is a somewhat elongate body of water approximately 46 kilometers in length and about 19.5 kilometers wide at its greatest diameter. It opens to the sea at the south, and along part of the eastern boundary there is appreciable water exchange with Vineyard Sound through the channels that separate the Elizabeth Islands. There is also some water exchange with Cape Cod Bay by means of the Cape Cod Canal (not shown in Fig. 1).

The Bay, as a whole, is relatively shallow, averaging only 11 meters in depth. Bottom temperatures vary from a maximum of approximately 22°C in summer to about 2°C in winter, while salinity values range from 29.5 to 32.5‰.

The locations and depths of the nineteen stations included in this study are shown in Figure 1.

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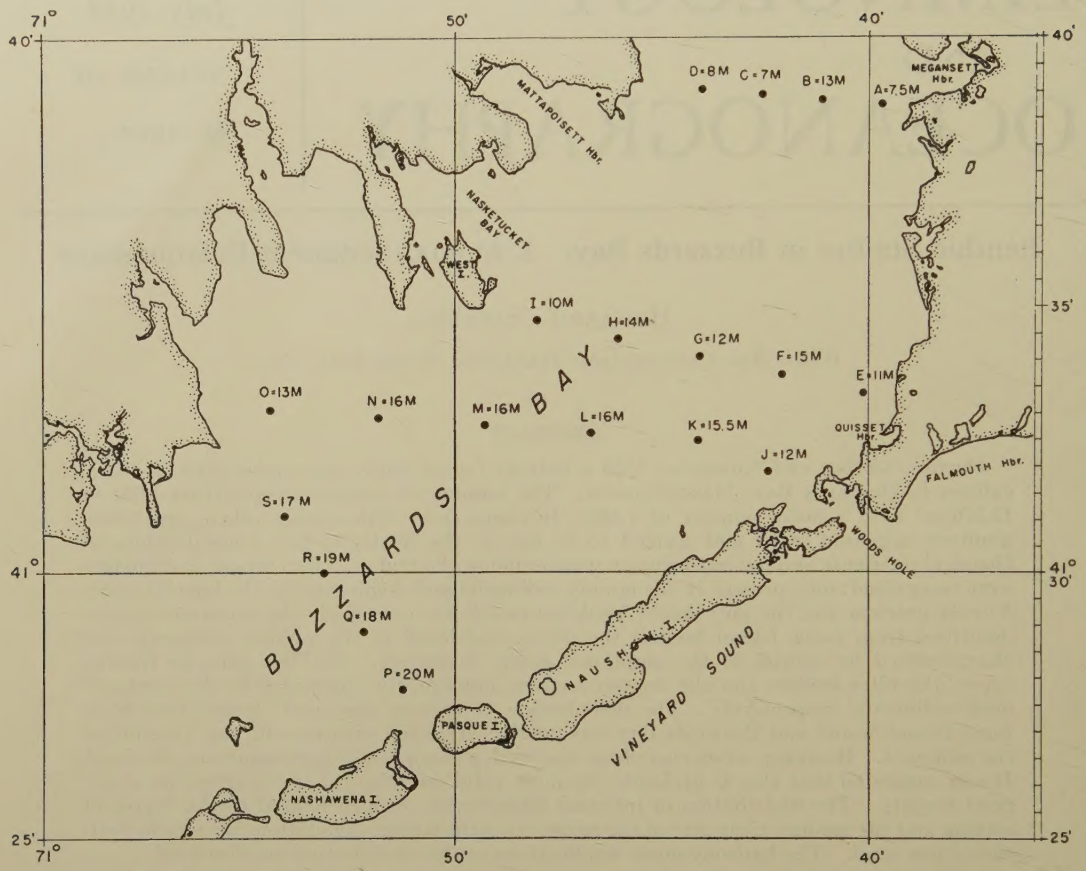


FIG. 1. Map of Buzzards Bay showing the locations and depths of the stations represented in the survey.

## METHODS

Samples were obtained with a Forster anchor dredge that was modified by welding the entire frame into a single unit. The apparatus was calibrated to dig to the depth of 7.6 cm, and a small-meshed burlap bag attached to the frame retained the sediment. A small portion of the sediment was saved for sediment analysis, and the volume of the remainder was measured before washing the contents through a sieve of 0.5 mm aperture. The animals retained on the screen were carefully picked out alive in the laboratory and preserved in formalin.

A graded series of sieves was used to divide the sands and gravels into seven size categories. The five silt fractions and the clays were determined by pipetting (Soil Survey Staff 1951). The silt components consisted predominantly of feldspar and some quartz, and the absence of clay particle aggregates indicated that the dispersing agent, sodium hexametaphosphate, was effective. The clay fraction, analyzed by Dr. Ivan Milne of the Gulf Research Development Company, consisted predominantly of illite and chlorite. Montmorillonite, kaolonite, feldspar, and quartz were also detected. The results of the mechanical analyses are given in Table 1. Silt-clay percentages, median grain sizes, and sorting coefficients are given in Table 2. The sorting value was obtained by dividing the variation between the 20 and 80 percentiles by two.

## FAUNAL ANALYSES

The numbers present at each station are given in Table 2. The mean number of organisms at all the stations is 4,430/m$^2$,

TABLE 1. *The particle size analysis by per cent weight of the 19 stations included in the Buzzards Bay survey*

| Station | Gravel | | Sand | | | | | Silt | | | | | Clay (>2μ) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | (8.0–4.0 (mm) | (3.9–2.0 mm) | (1.9–1.0 mm) | (0.9–0.5 mm) | (0.49–0.25 mm) | (0.24–0.125 mm) | (0.124–0.062 mm) | (61–31 μ) | (30–16 μ) | (15–8 μ) | (7–4 μ) | (3–2 μ) | |
| A | 2.04 | 4.76 | 14.63 | 53.74 | 20.48 | 2.58 | 0.74 | ← | ——— | 0.99 | ——— | → | |
| B | 0.29 | 0.46 | 4.98 | 23.14 | 44.20 | 17.16 | 3.76 | ← | ——— | 5.82 | ——— | → | |
| C | 1.41 | 1.62 | 5.46 | 31.30 | 48.32 | 8.85 | 0.35 | ← | ——— | 3.00 | ——— | → | |
| D | 0.14 | 0.20 | 1.86 | 14.52 | 43.40 | 33.70 | 2.06 | ← | ——— | 4.02 | ——— | → | |
| E | — | 0.27 | 5.16 | 35.06 | 49.30 | 7.62 | 0.28 | ← | ——— | 2.20 | ——— | → | |
| F | — | — | 0.06 | 0.30 | 1.43 | 2.62 | 4.37 | 10.66 | 18.38 | 20.35 | 12.57 | 9.85 | 19.55 |
| G | — | 0.07 | 1.73 | 13.66 | 34.19 | 32.96 | 2.13 | 1.05 | 3.18 | 3.00 | 2.47 | 1.12 | 4.19 |
| H | — | 0.21 | 3.49 | 26.70 | 46.05 | 13.40 | 2.33 | 0.92 | 0.78 | 1.05 | 1.86 | 0.97 | 2.42 |
| I | 3.34 | 3.58 | 8.99 | 19.92 | 30.16 | 21.85 | 4.48 | 2.09 | 0.93 | 0.93 | 1.07 | 0.42 | 2.20 |
| J | — | 0.06 | 0.43 | 3.47 | 7.39 | 7.11 | 15.65 | 14.35 | 11.53 | 8.69 | 10.33 | 6.41 | 14.28 |
| K | — | — | — | — | 0.10 | 0.21 | 1.78 | 10.75 | 16.93 | 22.23 | 22.23 | 8.00 | 17.47 |
| L | — | — | 0.05 | 0.12 | 0.27 | 1.67 | 4.21 | 23.50 | 14.13 | 13.52 | 13.73 | 10.05 | 19.10 |
| M | — | — | — | 0.04 | 0.23 | 0.93 | 5.45 | 11.96 | 18.63 | 17.67 | 16.51 | 9.52 | 18.70 |
| N | — | 0.06 | 1.24 | 9.18 | 40.48 | 42.18 | 2.30 | 0.89 | 0.18 | 0.53 | — | 0.71 | 2.21 |
| O | 1.09 | 1.16 | 1.25 | 1.29 | 2.24 | 3.37 | 15.99 | 16.45 | 15.17 | 14.26 | 10.79 | 4.20 | 12.57 |
| P | — | 0.06 | 0.04 | 0.32 | 12.50 | 78.05 | 4.04 | 0.79 | 0.54 | 1.58 | 1.20 | 0.52 | 0.38 |
| Q | — | — | 0.06 | 0.45 | 0.68 | 5.96 | 20.87 | 13.62 | 14.53 | 13.05 | 12.72 | 6.62 | 11.40 |
| R | — | 0.20 | 0.12 | 0.28 | 0.84 | 1.36 | 5.27 | 17.23 | 20.09 | 16.87 | 7.19 | 12.22 | 18.18 |
| S | 1.24 | 0.19 | 1.23 | 4.27 | 12.57 | 19.43 | 10.04 | 9.87 | 11.72 | 6.47 | 8.51 | 2.90 | 11.59 |

TABLE 2. *The values of certain geological and ecological factors measured in the survey*

| Station | Silt-clay percentage | Clay percentage | Sorting coefficient (mm) | Median grain size (mm) | No. Animals /m² | Epifauna | | Filter-feeding infauna | | | | Deposit-feeding infauna | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | No./m² | % of total | No./m² | % of total | No. dominant spp. /m²* | % of total filter-feeders | No./m² | % of total | No. dominant spp. /m²** | % of total deposit-feeders |
| A | 0.99 | | 0.67 | 0.68 | 1629 | 745 | 45.73 | 295 | 33.27 | 124 | 42.03 | 233 | 26.35 | 0 | 0.00 |
| E | 1.79 | | 0.48 | 0.45 | 2259 | 115 | 5.09 | 980 | 45.71 | 837 | 85.41 | 227 | 10.59 | 213 | 93.84 |
| C | 3.00 | | 0.50 | 0.44 | 3305 | 450 | 13.62 | 1841 | 64.48 | 1765 | 95.87 | 363 | 12.71 | 0 | 0.00 |
| D | 3.81 | | 0.31 | 0.31 | 3283 | 191 | 5.82 | 2371 | 76.68 | 2007 | 84.65 | 321 | 10.38 | 136 | 42.37 |
| N | 4.40 | | 0.30 | 0.26 | 5859 | 125 | 2.13 | 4648 | 81.06 | 3945 | 84.22 | 687 | 11.97 | 30 | 4.37 |
| P | 5.00 | | 0.10 | 0.18 | 12576 | 5290 | 42.06 | 5185 | 62.91 | 3114 | 60.06 | 3084 | 34.72 | 941 | 30.51 |
| B | 5.32 | | 0.45 | 0.37 | 2619 | 179 | 6.83 | 1761 | 72.17 | 1452 | 82.45 | 258 | 10.57 | 189 | 73.26 |
| I | 6.68 | | 0.70 | 0.38 | 4379 | 437 | 9.98 | 2575 | 65.32 | 2186 | 84.79 | 426 | 10.81 | 315 | 73.94 |
| H | 6.90 | | 0.45 | 0.37 | 5519 | 179 | 3.24 | 3227 | 60.43 | 2855 | 88.49 | 1539 | 28.82 | 448 | 29.10 |
| G | 13.29 | 4.19 | 0.34 | 0.26 | 3061 | 33 | 0.11 | 1497 | 49.44 | 739 | 49.37 | 1423 | 46.99 | 1004 | 73.37 |
| | | | | | 44489 | | | 24380 | x̄=64.87 | 19024 | x̄=78.03 | 8561 | x̄=22.79 | 3316 | x̄=38.73 |
| S | 43.64 | 11.59 | 0.26 | 0.04 | 4319 | 267 | 6.18 | 1362 | 33.61 | 1002 | 73.51 | 1845 | 45.53 | 1578 | 85.58 |
| J | 59.42 | 12.35 | 0.089 | 0.03 | 5455 | 447 | 8.19 | 2072 | 41.29 | 1238 | 59.75 | 2836 | 56.52 | 2272 | 80.11 |
| Q | 63.00 | 11.40 | 0.080 | 0.023 | 3211 | 57 | 1.78 | 620 | 19.31 | 55 | 8.87 | 2391 | 74.46 | 1955 | 81.76 |
| O | 67.14 | 12.52 | 0.079 | 0.023 | 4462 | 0 | 0.00 | 405 | 9.08 | 0 | 0.00 | 3892 | 87.23 | 3758 | 96.56 |
| R | 81.19 | 18.18 | 0.038 | 0.013 | 6068 | 126 | 2.08 | 125 | 2.10 | 0 | 0.00 | 5545 | 93.32 | 4527 | 81.61 |
| M | 83.95 | 18.70 | 0.029 | 0.010 | 5934 | 146 | 2.46 | 104 | 1.80 | 62 | 59.62 | 5632 | 97.30 | 5173 | 91.85 |
| F | 85.47 | 19.45 | 0.029 | 0.010 | 1187 | 0 | 0.00 | 41 | 3.45 | 8 | 19.51 | 1049 | 88.37 | 737 | 70.26 |
| L | 86.23 | 19.10 | 0.042 | 0.012 | 7982 | 182 | 2.30 | 377 | 4.87 | 109 | 28.91 | 7089 | 91.52 | 6114 | 86.25 |
| K | 93.36 | 17.45 | 0.020 | 0.015 | 1064 | 18 | 1.69 | 215 | 20.55 | 106 | 49.30 | 742 | 70.94 | 673 | 90.70 |
| | | | | | 39628 | | | 5321 | x̄=13.81 | 2580 | x̄=48.49 | 26787 | x̄=78.35 | 26787 | x̄=86.35 |

* *Ampelisca spinipes, A. macrocephala, Byblis serrata, Cerastoderma pinnulatum.*

** *Tellina tenera, Nephthys incisa, Nucula proxima, Turbonilla* sp., *Retusa caniculata, Cylichna orzya, Nerinides* sp.

with a range of from 1,064 at Station K to 12,516 at Station P.

Buzzards Bay has numerically smaller benthic populations than some other areas. This is shown in the following table.

| Location | No. of stations | Range | Mean | Screen mesh size |
|---|---|---|---|---|
| Buzzards Bay (present study) | 19 | 1,064–12,576 | 4,430 | 0.5 |
| Loch Craiglin, Scotland (Raymont 1949) | 5 | 5,409–19,065 | 14,275 | 1.0 |
| English Channel (Mare 1942) | 1 | | 2,356 | 1.0 |
| Long Island Sound (Sanders 1956) | 8 | 5,566–46,404 | 16,446 | 1.0 |

The Buzzards Bay-Woods Hole environment can be compared with Long Island Sound (Riley 1955, Sanders 1956) in regard to at least a limited number of factors. Chlorophyll readings (Yentsch, unpublished) and phosphorus concentrations (Crowin, unpublished) have been collected from the dock of the Woods Hole Oceanographic Institution. From the nature of the local current system it is apparent that such samples are fairly typical of the water present in the surrounding regions, and the values measured, therefore, can be applied directly to Buzzards Bay. The mean depth of Long Island Sound is 20 meters and of Buzzards Bay 11 meters. Yet Long Island Sound exceeds Buzzards Bay in winter maximum phosphorus, average chlorophyll/$m^3$, and mean benthic population by factors of 2.5, 3.5, and 3.6, respectively. It seems obvious that since the depth is not markedly different in these two areas, the very much larger bottom population present in Long Island Sound is the result of the larger phytoplankton population, its major source of food.

## BENTHIC COMMUNITIES IN BUZZARDS BAY

One of the main objectives of this paper is to delimit the level-bottom animal communities present in Buzzards Bay. To facilitate this end, the distribution by num-

TABLE 3. *The numbers and proportion of 8 species of animals commonly associated with sandy sediments in Buzzards Bay*

| Station | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | | 7 | | 8 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % |
| A | 124 | 7.61 | — | — | — | — | — | — | — | — | 62 | 3.81 | 15 | 0.92 | 78 | 4.79 |
| E | 14 | 0.62 | 57 | 2.52 | 28 | 1.24 | 738 | 32.67 | 14 | 0.62 | 419 | 18.55 | 85 | 3.76 | 114 | 5.05 |
| C | 1715 | 51.89 | 50 | 1.51 | — | — | — | — | — | — | 275 | 8.32 | 75 | 2.27 | 25 | 0.76 |
| D | 1628 | 49.59 | 322 | 9.81 | 57 | 1.74 | — | — | 136 | 4.14 | 336 | 10.23 | 64 | 1.95 | 14 | 0.43 |
| N | 98 | 1.67 | 823 | 14.22 | 2720 | 46.42 | 294 | 5.02 | 6 | 0.10 | 74 | 1.26 | 270 | 4.61 | 25 | 0.48 |
| P | 566 | 7.77* | 849 | 11.65 | 1520 | 20.89 | 179 | 2.41 | 92 | 1.26 | 238 | 3.27 | 209 | 2.87 | — | — |
| | | 4.50** | | 6.75 | | 12.09 | | 1.42 | | 0.73 | | 1.89 | | 1.66 | | |
| B | 1306 | 49.87 | 129 | 4.93 | 17 | 0.65 | — | — | 189 | 7.22 | 258 | 9.85 | 266 | 10.16 | 34 | 1.30 |
| I | 928 | 21.20 | 91 | 2.08 | 22 | 0.50 | 1145 | 26.14 | 229 | 5.23 | 22 | 0.50 | 480 | 10.96 | 437 | 9.98 |
| H | 471 | 8.53 | 90 | 1.63 | — | — | 1394 | 25.26 | 362 | 6.56 | 36 | 0.65 | 615 | 11.14 | 326 | 5.91 |
| G | 439 | 14.34 | 54 | 1.76 | 11 | 0.30 | — | — | 268 | 8.76 | 32 | 1 05 | 64 | 2.09 | — | — |
| | 7289 | $\bar{x}$=18.59 | 2475 | $\bar{x}$=6.31 | 4375 | $\bar{x}$=11.16 | 3750 | $\bar{x}$=9.39 | 1296 | $\bar{x}$=3.29 | 1752 | $\bar{x}$=4.47 | 2143 | $\bar{x}$=5.47 | 1053 | $\bar{x}$=2.69 |
| S | 639 | 14.80 | 303 | 7.02 | 60 | 1.39 | — | — | 218 | 5.05 | 36 | 0.83 | 36 | 0.83 | 72 | 1.67 |
| J | 455 | 8.34 | — | — | — | — | 789 | 14.46 | — | — | — | — | — | — | 55 | 1.01 |
| Q | — | — | — | — | — | — | 55 | 1.71 | — | — | — | — | 11 | 0.34 | 11 | 0.34 |
| O | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| R | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 204 | 3.36 |
| M | 10 | 0.17 | — | — | — | — | 52 | 0.87 | — | — | — | — | — | — | 42 | 0.71 |
| F | 8 | 0.63 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| L | 36 | 0.45 | — | — | — | — | 73 | 0.92 | — | — | — | — | — | — | 182 | 2.30 |
| K | 9 | 0.85 | — | — | — | — | 97 | 9.12 | — | — | — | — | — | — | 36 | 3.38 |
| | 1157 | $\bar{x}$= 2.92 | 303 | | 60 | | 1066 | $\bar{x}$=2.69 | 218 | | 36 | | 47 | | 602 | $\bar{x}$=1.52 |

1. *Ampelisca spinipes*
2. *Ampelisca macrocephala*
3. *Byblis serrata*
4. *Cerastoderma pinnulatum*
5. *Tellina tenera*
6. *Nephthys bucera*
7. *Glycera americana*
8. *Lumbrinereis tenuis*

* Percent of infauna.
** Percent of total fauna.

ber of the abundant species is arranged according to the increasing silt and clay content of the sediment (see Tables 3 and 4. Since Station P alone carried a numerically significant epifaunal population, it was necessary to designate for that station in Table 3 both an infaunal and total faunal column.) Certain of these dominant species are wholly or largely limited to sediments with small amounts of silts and clays (*Ampelisca spinipes*, *A. macrocephala*, *Byblis serrata*, *Tellina tenera*, *Nephthys bucera*, and *Glycera* sp.), while others (*Nucula proxima*, *Nephthys incisa*, *Nerinides* sp., *Retusa caniculata*, and *Cylichna orzya*) are largely confined to soils with large concentrations of silts and clays. Other animals such as *Ninöe nigripes*, *Lumbrinereis* sp., and, less strikingly, *Unciola irrorata*, are more widely distributed.

It seems possible from this distribution that two faunal assemblages can be recognized, one found in sediments with low concentrations of fine particles and represented in the survey by Stations A, E, C, D, N, P, B, I, H, and G, the other in sediments with large concentrations of silts and clays and represented by Stations S, J, Q, O, R, M, F, L, and K. Certain stations in the middle of the soil spectrum show transitions from one assemblage to the other; for example, Station G contained appreciable numbers of *Nephthys incisa*, while *Tellina tenera* and *Ampelisca macrocephala* were abundant at Stations S and J.

It is usual to describe benthic communities after the manner of Petersen (1913) by combining the names of two of the characteristic species. Such dominant species should both be numerous and belong to different taxonomic units.

The soft-bottom association is essentially the same as the *Nephthys incisa-Yoldia limatula* community described from Long Island Sound (Sanders 1956). The common representatives in Buzzards Bay are listed below. The percentage composition is given only

TABLE 4. *The numbers and proportion of 8 species of animals commonly associated with muddy sediments in Buzzards Bay*

| Station | 1 | | 2 | | 3 | | 4 | | 5 | | 6 | | 7 | | 8 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % | No. | % |
| A | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 31 | 1.09 |
| E | — | — | — | — | — | — | — | — | — | — | — | — | 24 | 1.06 | — | — |
| C | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 138 | 4.18 |
| D | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 50 | 1.52 |
| N | — | — | 24 | 0.41 | — | — | — | — | — | — | — | — | 25 | 0.43 | 123 | 2.10 |
| P | — | — | — | — | — | — | — | — | — | — | 15 | 0.21 | 641 | *5.10 | 224 | 3.35 |
| | | | | | | | | | | | | | | **8.80 | | 1.78 |
| B | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 9 | 0.31 |
| I | 10 | 0.23 | — | — | — | — | — | — | — | — | 44 | 1.00 | 32 | 0.73 | 33 | 0.75 |
| H | 16 | 0.29 | 16 | 0.29 | — | — | — | — | 54 | 0.98 | — | — | 326 | 5.91 | 18 | 0.33 |
| G | 755 | 24.67 | 10 | 0.33 | — | — | — | — | 11 | 0.36 | — | — | 117 | 3.82 | 21 | 0.69 |
| | 781 | $\bar{x}$=1.99 | 50 | | | | | | 65 | | 59 | | 1165 | $\bar{x}$=2.97 | 647 | $\bar{x}$=1.65 |
| S | 603 | 13.96 | 121 | 2.80 | — | — | 579 | 13.41 | 169 | 3.91 | 96 | 2.22 | 591 | 13.68 | 169 | 3.91 |
| J | 418 | 7.66 | 73 | 1.34 | 1218 | 22.33 | 36 | 0.66 | 218 | 4.00 | 91 | 1.67 | 127 | 2.33 | 273 | 5.00 |
| Q | 739 | 23.01 | 320 | 9.97 | 254 | 7.91 | 56 | 1.74 | 255 | 5.71 | 387 | 12.05 | 88 | 2.74 | 55 | 1.71 |
| O | 349 | 7.82 | 70 | 1.57 | 2162 | 48.45 | 28 | 0.63 | 698 | 15.64 | 251 | 5.63 | 147 | 3.29 | 237 | 5.31 |
| R | 869 | 14.32 | 3306 | 54.48 | — | — | 374 | 6.16 | 159 | 2.62 | 193 | 3.18 | 68 | 1.12 | — | — |
| M | 1385 | 23.34 | 2040 | 34.38 | — | — | 1145 | 19.30 | 312 | 5.26 | 291 | 4.90 | 52 | 0.88 | — | — |
| F | 445 | 35.88 | 49 | 3.86 | 16 | 1.26 | 65 | 5.13 | 146 | 10.51 | 16 | 1.26 | — | — | — | — |
| L | 1642 | 20.71 | 3378 | 42.61 | — | — | 389 | 4.91 | 304 | 3.83 | 401 | 5.06 | 97 | 1.22 | — | — |
| K | 340 | 31.95 | 88 | 8.27 | — | — | 45 | 4.23 | 116 | 10.90 | 80 | 7.52 | 27 | 2.54 | — | — |
| | 6790 | $\bar{x}$=17.13 | 9445 | $\bar{x}$=23.83 | 3650 | $\bar{x}$=9.21 | 2717 | $\bar{x}$=6.85 | 2377 | $\bar{x}$=6.00 | 1806 | $\bar{x}$=4.56 | 1197 | $\bar{x}$=3.01 | 734 | $\bar{x}$=1.85 |

1. *Nephthys incisa*
2. *Nucula proxima*
3. *Turbonilla* sp.
4. *Nerinides* sp.
5. *Retusa caniculata*
6. *Cylichna orzya*
7. *Ninöe nigripes*
8. *Unciola irrorata*

* Percent of infauna.
** Percent of total fauna.

for those species comprising more than one per cent of the population.

| | % composition | | % composition |
|---|---|---|---|
| Polychaeta | | Lamellibranchia | |
| *Nephthys incisa* | 17.13 | *Nucula proxima* | 23.83 |
| *Nerinides* sp. | 6.85 | *Cerastoderma pinnulatum* | 2.69 |
| *Ninöe nigripes* | 3.01 | *Pitar morrhuana* | 2.55 |
| *Lumbrinereis tenuis* | 1.52 | *Yoldia limatula* | |
| *Tharyx acutus* | 1.08 | Gastropoda | |
| *Exogone dispar* | | *Turbonilla* sp. | 9.21 |
| *Lumbrinereis hebes* | | *Retusa caniculata* | 6.00 |
| *Aricidea* sp. | | *Cylichna orzya* | 4.56 |
| *Scolelipedes* sp. | | *Nassarius triviattatus* | |
| *Maldanopsis elongata* | | *Bela turricola* | |
| *Melinna cristata* | | Enteropneusta | |
| Crustacea | | *Dolichoglossus kowalevskii* | |
| *Ampelisca spinipes* | 2.92 | Tunicata | |
| *Unciola irrorata* | 1.85 | *Molgula complanata?* | |
| *Hutchinsoniella macracantha* | | | |
| *Edotea montosa* | | | |

The two most common forms are *Nephthys incisa* and *Nucula proxima*, comprising 17.13 and 23.83 % of the population by number. Since *Yoldia limatula* makes a much less significant numerical contribution in Buzzards Bay, it is proposed that *Nucula proxima* replace it as a characterizing dominant. The upper salinity associated with this community in Long Island Sound was 29.2, in Buzzards Bay 32‰. The other environmental conditions associated with this community have been described elsewhere (Sanders 1956)

The predominantly sand assemblage is clearly characterized by three closely related species of amphipods, *Ampelisca spinipes*, *A. macrocephala*, and *Byblis serrata* which together constitute over 36 % of the community. The remaining really abundant species in this association is the lamellibranch, *Cerastoderma pinnulatum*, which comprised more than 10 % of the population at the time of sampling. However, because this organism is an annual, being present in markedly reduced numbers or even absent during a significant fraction of the year, it is a poor characterizing species. It therefore seems reasonable to designate this sand bottom association as the *Ampelisca* spp. community, which in Buzzards Bay is found in sediments containing less than 35-45 % silt-clay. The common representatives are listed below. The per cent composition is given only for those species comprising more than one per cent of the population.

| | % composition | | % composition |
|---|---|---|---|
| Polychaeta | | *Leptocheirus pingius* | |
| *Glycera americana* | 5.47 | *Cerapus tubularis* | |
| *Nephthys bucera* | 4.47 | *Corophium* spp. | |
| *Ninöe nigripes* | 2.97 | *Ptilanthura tenuis* | |
| *Lumbrinereis tenuis* | 2.69 | *Edotea montosa* | |
| *Nephthys incisa* | 1.99 | *Stenothöe* sp. | |
| *Sthenelais boa* | | *Batea secunda* | epifauna |
| *Pholöe minuta* | | *Erichthonius brasiliensis* | epifauna |
| *Eteone lacta* | | *Aeginella longicornis* | epifauna |
| *Phyllodoce arenae* | | *Crago septemspinosus* | epifauna |
| *Paraspionosyllis longicirrata* | | *Pagurus annulipes* | epifauna |
| *Podarke obscura* | | *Neopanope texana* | epifauna |
| *Nereis zonata* | | Lamellibranchia | |
| *Diopatra cuprea* | | *Cerastoderma pinnulatum* | 10.17 |
| *Haploscolopos fragilis* | | *Tellina tenera* | 3.29 |
| *Pista* sp. | | *Nucula delphinodonta* | |
| *Polycirrus eximus* | | *Pandora gouldiana* | |
| *Ampharete arctica* | | *Lyonsia hyalina* | |
| *Scalibregma inflatum* | | *Laevocardium mortoni* | |
| Crustacea | | *Ensis directus* | |
| *Ampelisca spinipes* | 18.59 | Gastropoda | |
| *Byblis serrata* | 11.31 | *Natica pusilla* | |
| *Ampelisca macrocephala* | 6.31 | *Nassarius triviattatus* | |
| *Unciola irrorata* | 1.65 | *Crepidula plana* | epifauna |
| *Oxyurostylis smithi* | | *Mitrella lunata* | epifauna |
| *Paraphoxus spinosus* | | *Anachis avara* | epifauna |
| *Phoxocephalus holbölli* | | Tunicata | |
| | | *Molgula complanata?* | 1.85 |

The same community with most of the same species represented also occurs in the sandy sediments of Long Island Sound where the *Ampelisca* species comprised about 32 % of the fauna. Since too few stations of this type were present in the survey (Stations 1, 4, and Charles Island), the writer did not feel justified in naming the association in Long Island Sound. In view of the faunal analyses in Buzzards Bay, however, it seems apparent that the infauna of the sandy sediments of Long Island Sound also belongs to the *Ampelisca* spp. community. Evidence for the presence of similar communities elsewhere can be found in the studies of Miyadi (1940), who observed that an *Ampelisca* species was a common organism in the sandy sediments of Tanabe-wan and Osaka-wan, two somewhat enclosed Japanese Bays.

Certain differences exist in the species composition of the ampeliscids in the Long Island Sound and Buzzards Bay regions. *Ampelisca macrocephala* and *Byblis serrata* are largely absent from the region investigated in the central Long Island Sound area. Instead, two sibling species, designated tentatively by the writer as *Ampelisca A* and *B*, comprise the dominant ampeliscid species of the region. Both forms appear identical morphologically, differing only in size, the former being approximately three times as heavy as the latter. There is little overlap in the distribution of the species, with *Ampelisca A* present in sediments with relatively less silt and clay. Probably both forms have been lumped together and included in the species *Ampelisca spinipes*. (Taxonomic difficulties involved in the genus *Ampelisca* have been discussed in detail by Reid 1951.)

There is some indication that *Ampelisca spinipes* in Buzzards Bay may be composed of the same two components, although there appears to be more overlap in the distributions which tend to blur size differences. To test this contention, size-frequency distributions of the *Ampelisca spinipes* representatives were constructed for the nine samples having adequate numbers of this form. The mean length of the largest 20% in each of the four stations having the least silt-clay content was appreciably larger than any of the remaining five stations. Converting length to dry weight (Sanders 1956) the average dry weight equivalent of the largest 20% of the population at the four stations with less silt-clay was approximately 2.8 times as large as the mean dry weight equivalent of the other five stations. These data at least imply that both

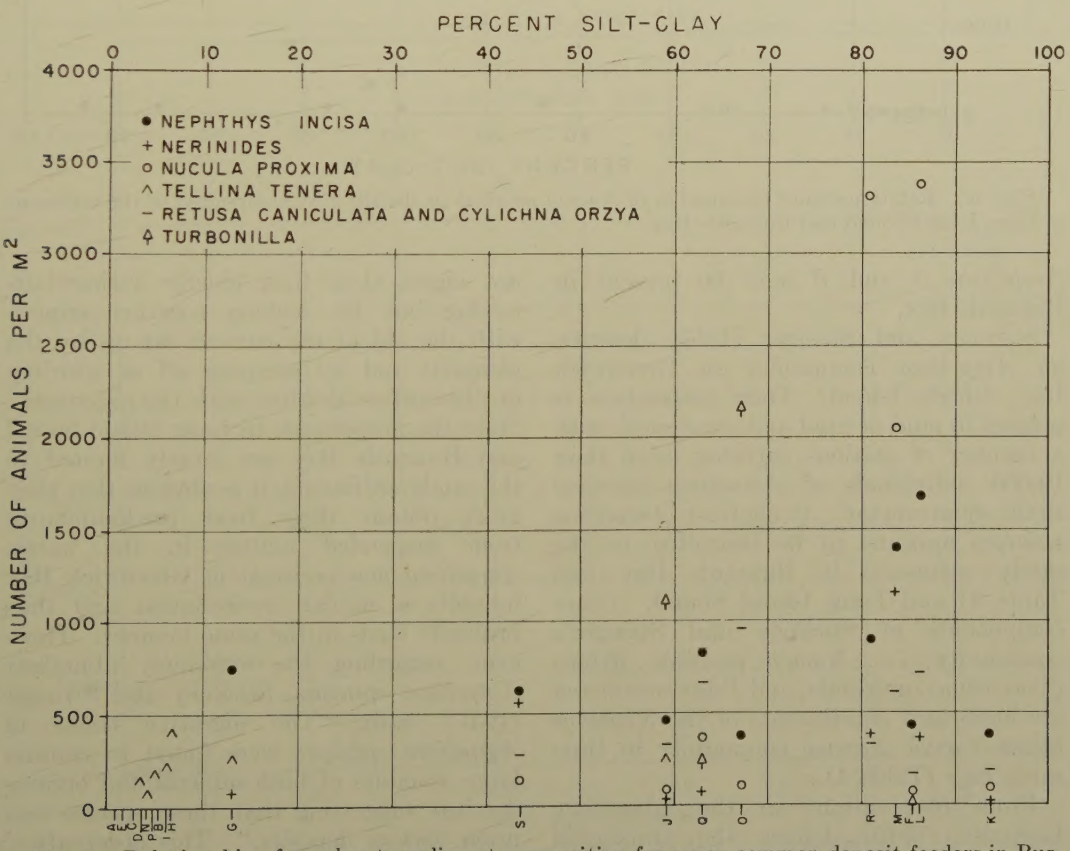


FIG. 2. Relationship of number to sediment composition for seven common deposit-feeders in Buzzards Bay.

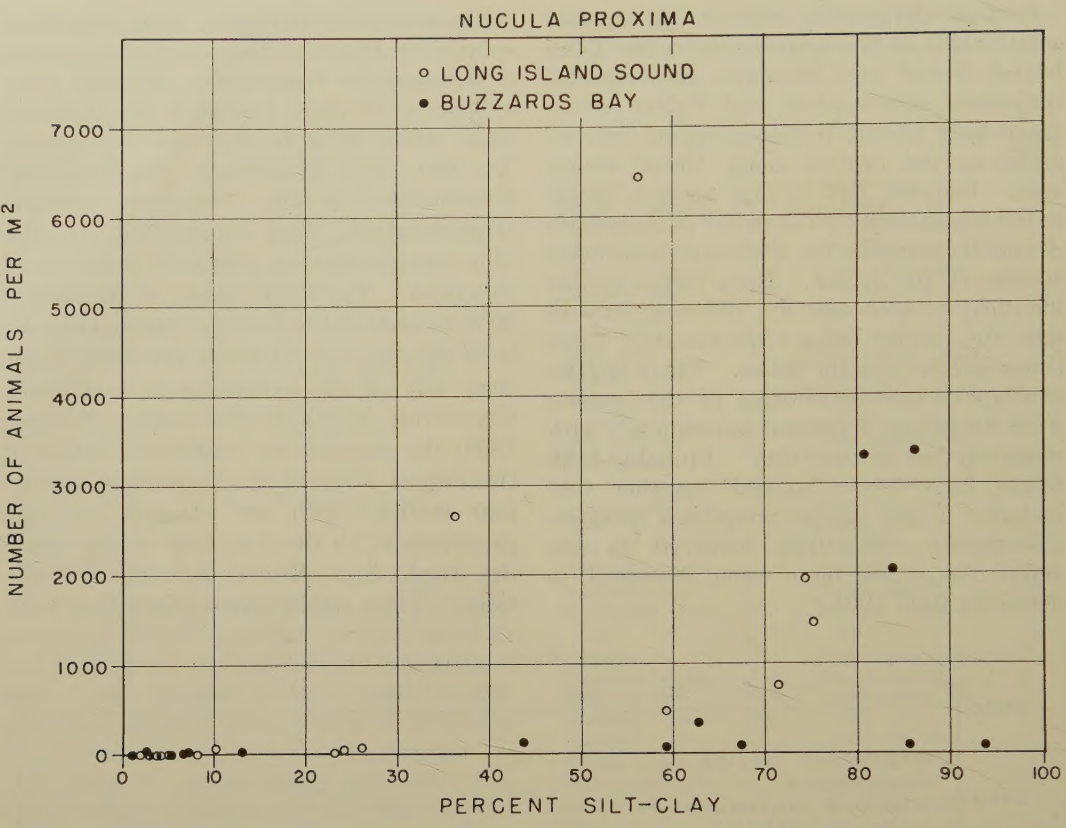


FIG. 3a. Relationship of the number of *Nucula proxima* to the silt-clay component of the sediment in Long Island Sound and Buzzards Bay.

*Ampelisca A* and *B* may be present in Buzzards Bay.

Stickney and Stringer (1957) describe an *Ampelisca* community in Greenwich Bay, Rhode Island. Their association is present in mud or mud and some sand, with a number of stations carrying more than 10,000 individuals of *Ampelisca spinipes* to the square meter. In contrast, *Ampelisca spinipes* appears to be restricted to the sandy sediments in Buzzards Bay (see Table 3) and Long Island Sound. Other components of Stickney and Stringer's community, *i.e.*, *Nucula proxima*, *Retusa* (Tornatina) *caniculata*, and *Pitar morrhuana* are important constituents of the *Nephthys incisa-Nucula proxima* community in Buzzards Bay (Table 4).

From observations in the laboratory Enequist (1949) defines the ampeliscid type of feeding in which the animals "do not ingest their food chiefly during burrowing but by sucking together tripton with the aid of the current set up by the pleopods and by scraping off or whirling up the surface detritus with the antennae." Since the ampeliscids in Long Island Sound and Buzzards Bay are largely limited to the sandy sediments, it is obvious that they must obtain their food predominantly from suspended matter in the water. *Ampelisca macrocephala* in Greenwich Bay inhabits a similar environment and thus probably feeds in the same manner. However, regarding the extremely abundant *Ampelisca spinipes*, Stickney and Stringer (1957) state, "The digestive tracts of *Ampelisca spinipes* were found to contain large amounts of both mineral and organic detritus suggesting that these species feed upon bottom deposits." This observation, together with the fact that the animal is

most abundant in the softer deposits, indicates that in Greenwich Bay, *Ampelisca spinipes* obtains its food largely from settled detritus secondarily suspended by the animal's activity. Conceivably, *Ampelisca spinipes* of Greenwich Bay may be the same animal as *Ampelisca B* in Long Island Sound, since the latter form is found in finer sediments than *Ampelisca A*. Finally, it should be noted that the *Ampelisca* community of Greenwich Bay is replaced in Long Island Sound and Buzzards Bay by the *Nephthys incisa-Nucula proxima* community, which has an extremely small ampeliscid component.

## ANIMAL-SEDIMENT RELATIONSHIPS

The primary consumers, *i.e.*, herbivores and detritus feeders, usually comprise 80–99% by number of the benthic faunal in Buzzards Bay. The filter-feeders or animals that obtain their food from suspended matter make up the majority of the fauna in the sandy sediments, while the deposit-feeders living on organic matter in or on the bottom dominate the fauna in the finer sediments. In the *Ampelisca* spp. community the filter-feeders comprise almost two-thirds of the population by number, while over 80% of the fauna of the *Nephthys incisa-Nucula proxima* community are deposit-feeders. The sand sediment, where the *Ampelisca* spp. community is found, reflects the more pronounced current activity in such environments which in turn brings more potential food to the filter-feeding organisms than would weaker currents. Conversely, over mud bottoms, the feeble currents allow organic matter to settle out, thus providing an adequate source of nutrition for large numbers of deposit-feeders.

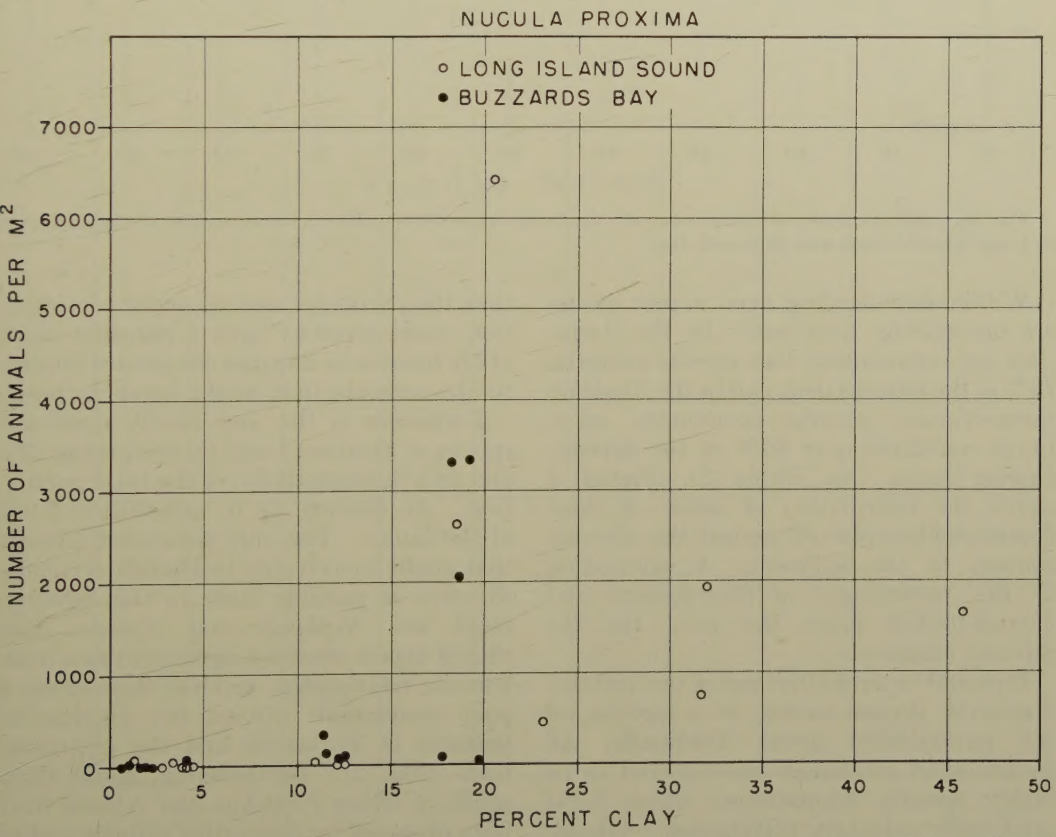


FIG. 3b. Relationship of the number of *Nucula proxima* to the clay component of the sediment in Long Island Sound and Buzzards Bay.

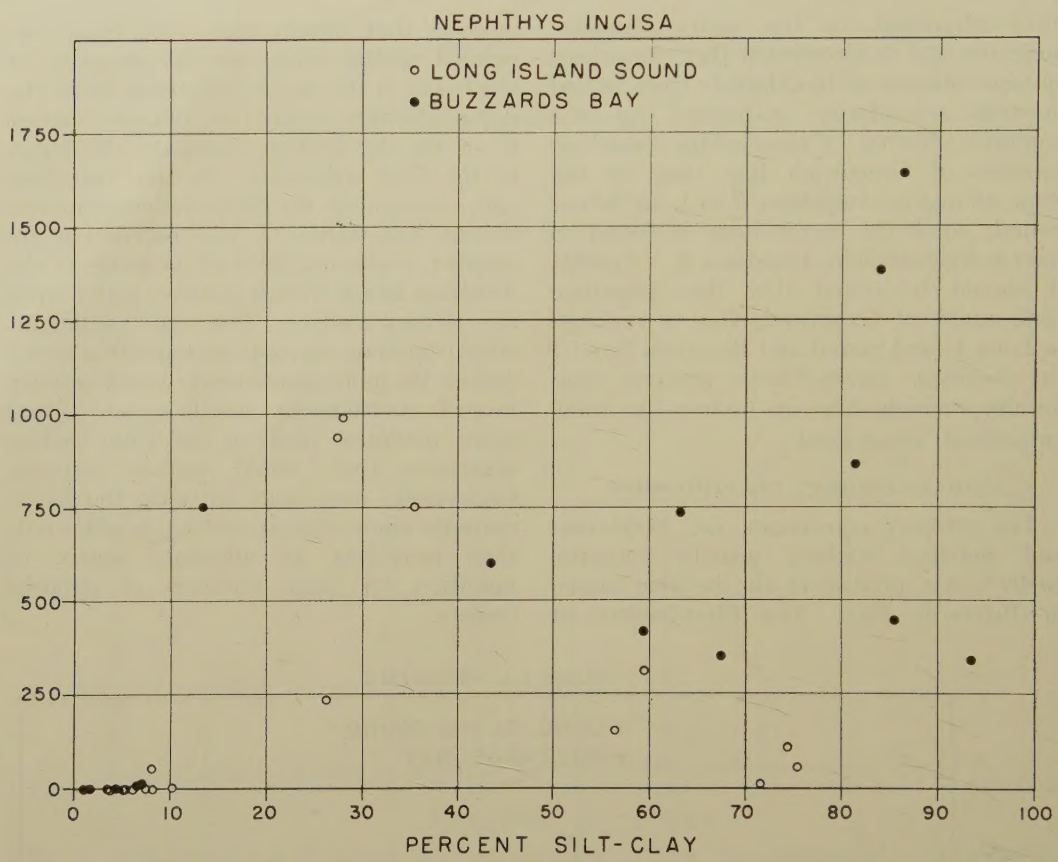


FIG. 4a. Relationship of the number of *Nephthys incisa* to the silt-clay component of the sediment in Long Island Sound and Buzzards Bay.

Within each feeding type a few species are numerically dominant. In the *Ampelisca* spp. community four species comprise 78% of the filter-feeders, and in the *Nephthys incisa-Nucula proxima* community seven forms constitute over 86% of the deposit-feeding fauna (see Table 2). Figure 2 shows the distribution of seven of these deposit-feeders plotted against the silt-clay content of the sediment. A summation of the percentages of filter-feeders and deposit-feeders gives the total for the primary consumers.

It should be noted that one of the included dominant deposit-feeders is a species of the pyramidellid genus *Turbonilla*. All pyramidellid gastropods are believed to be highly specific ectoparasites whose hosts are usually sedentary polychaetes, molluscs, and coelenterates (Fretter and Graham 1949). Yet it is impossible to conceive that the particular species under consideration could possibly have a parasitic mode of life because of its great abundance relative to the animals that might serve as hosts.

*Turbonilla* is the numerically dominant species of Stations J and O, comprising 22.3 and 48.5%, respectively, of the total population. At Station Q it constitutes 7.9% of the fauna. The only associated animals that might conceivably be abundant enough to serve as possible hosts in this environment are *Nephthys* and *Nucula*. One should expect excellent agreement in a host-parasite relationship, and yet there exists a poor correlation between the distribution patterns of *Turbonilla* and the postulated hosts (Fig. 2). Furthermore, many thousands of living *Nephthys* and *Nucula* have been observed by this writer without finding any indication of a pyramidellid parasite. The actively burrowing habit of *Nephthys*

makes that animal an unlikely host, and it is unreasonable to suppose that the diminutive *Nucula* could serve as a suitable host for the larger and often more numerous *Turbonilla*. It is much more likely that this particular species of *Turbonilla* is not an ectoparasite but a deposit-feeder, using its buccal pump to draw in the extremely soft, organically-rich superficial sediment.

*The distribution of deposit-feeders in Buzzards Bay and Long Island Sound*

Realizing that the distribution of any species in nature is the result of a complex of environmental factors, a unifactorial analysis gives, at best, only a moderately good correlation. For example, the relationship between the distribution of certain deposit-feeding species and the fine fractions of the sediment can be modified in sediments of very high concentrations of these con-constituents by the reduction of oxygen.

The numerically abundant species of deposit-feeders are essentially the same in both of these regions, yet the greatest concentration in Buzzards Bay occurs in sediments with an appreciably higher fraction of silts and clays than in Long Island Sound, although the points are too few to demonstrate this statistically. Figure 3a shows the relationship between the silt-clay composition of the sediments and the numbers of *Nucula proxima*, the most abundant deposit-feeder in both regions. The Long Island Sound samples reveal high numerical values at from 35 to 60% silt-clay, while in Buzzards Bay the highest values are found between 80 to 87%, with low numbers in the region of Long Island Sound maximum.

The differences in distribution between the two areas are much more pronounced than that indicated in Figure 3a. Sediment

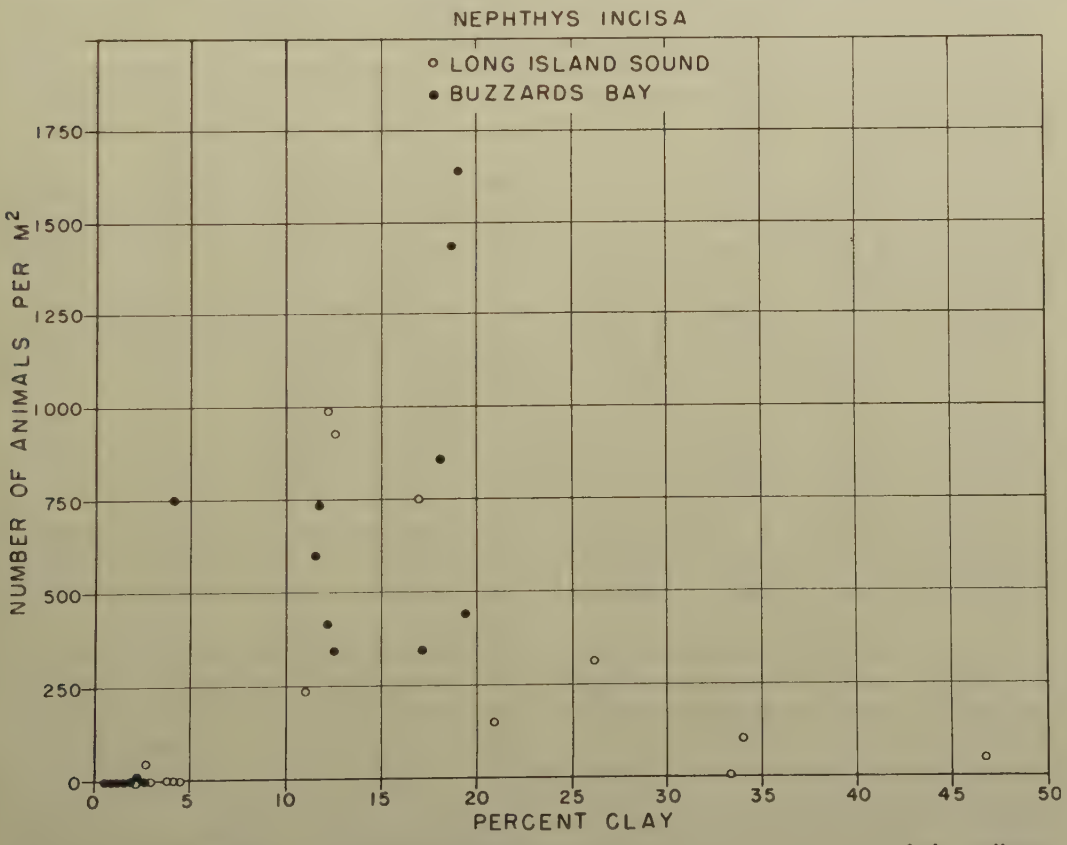


FIG. 4b. Relationship of the number of *Nephthys incisa* to the clay component of the sediment in Long Island Sound and Buzzards Bay.

analyses were not performed on all samples taken in the Long Island Sound study, particularly in regard to a number of samples from Stations 2, 7, and 8. However, the sediments that were analyzed (Sanders 1956) indicate that probably all samples from these stations had a silt-clay content that varied between 25 and 60 %. The number of *Nucula*/m² that were present in the samples not included in Figure 3a are given below. These help to confirm the existence of maximum populations in intermediate silt-clay percentages.

| | | |
|---|---|---|
| Station 7 | September 9, 1953 | 9,050 |
| | February 3, 1954 | 4,600 |
| | September 10, 1954 | 1,200 |
| Station 8 | August 1, 1953 | 4,100 |
| | February 3, 1954 | 8,000 |
| | July 23, 1954 | 10,000 |
| Station 2 | February 5, 1954 | 5,450 |

Essentially the same distributional pattern can be demonstrated for the next most abundant deposit-feeder, *Nephthys incisa* (Fig. 4a) except that the degree of difference in distribution is even more marked. Like *Nucula*, *Nephthys* in Buzzards Bay is found in largest numbers in 80 to 87 % silt-clay, although the polychaete is abundant over a wider sediment range than *Nucula*. By contrast, in Long Island Sound the largest populations of *Nephthys* are encountered in sediments of from 22 to 40 % silt-clay, while in sediments of more than 70 % silt-clay only small numbers are present.

Why should there be an apparent regional difference in the distribution patterns of *Nephthys* and *Nucula*? A closer scrutiny of the silt-clay fraction of the sediment in these two areas gives a clue. What is immediately evident is that the clay component of this fraction is much larger in the Long Island Sound samples, averaging 48.3 % with a range of from 37.8 to 61.2 %. On the other hand, in Buzzards Bay the clays average only 21.4 % of the silt-clay fraction with a minimum of 18.1 and a maximum of 26.9 %.

Much better agreement is obtained regarding the distribution of *Nucula* and *Nephthys* in Long Island Sound and Buzzards Bay if the number of animals is plotted against only the clay percentage (Figs. 3b and 4b). The Long Island Sound data show that the largest populations of *Nucula* are found between 16 and 22 % clay, and that appreciable numbers are present in sediments with greater clay concentrations. In Buzzards Bay almost the same sediment range, 16 to 19 % clay, representing some of the stations with the largest clay fractions, support the biggest populations of *Nucula*.

There is also excellent agreement in the distribution of *Nephthys* in Long Island Sound and Buzzards Bay (Fig. 4b). With the single exception of Station G with about 4 % clay, the largest populations seem to be confined to sediments with 10 to 20 % clay in both areas. At higher and particularly lower concentrations of clay the numbers of *Nephthys* rapidly diminish.

The data strongly suggest that clay is the most valid sediment correlate for the distribution of deposit-feeding organisms. Clays are much smaller than the silt particles and therefore have a relatively much larger surface area to bind organic matter, the source of food for deposit-feeders. Larger detrital components also tend to accumulate here due to the feeble currents. On the other hand, large concentrations of organic matter may reduce the oxygen content in the sediments and can ultimately limit the environment for deposit-feeders. It is no wonder that the clay fraction seems well correlated with the distribution of deposit-feeding animals.

### *The distribution of filter-feeding animals in Long Island Sound and Buzzards Bay*

The analyses of the samples in both regions demonstrate that the filter-feeders are the dominant feeding type in the sandy sediments, yet it is not entirely evident that the silt-clay concentration alone can explain their distribution pattern (see Table 2). The distribution of filter-feeders may be controlled by the hydrodynamic processes which determine the sediment - character rather than directly by the sediment. In the following theoretical speculations three processes need to be considered: the turbulence of water flow, the settling velocities

of particles, and the transport of particles. The current necessary to convert the laminar flow over the bottom into turbulent flow is dependent on two factors which are inversely related, the size of the grain protruding into the flow and the velocity of the current. This is shown as the roughness velocity in Figure 5 (Inman 1949). The larger the sediment particles the smaller the velocity necessary to convert a hydrodynamically smooth bottom to one that is hydrodynamically rough. The settling velocity of sediment particles is given by Stokes' Law for grains less than 0.18 mm diameter, and the relationship between particle size and velocity is linear. Particles larger than 0.18 mm fall more slowly than Stokes' Law might predict, because the turbulence created by the falling object becomes a factor (see Fig. 5). The velocity necessary to cause a particle to move along the bottom (threshold velocity, Fig. 5) is minimal for grain sizes of 0.18 mm. Smaller sizes act as a hydrodynamically smooth bottom, and the drag becomes distributed

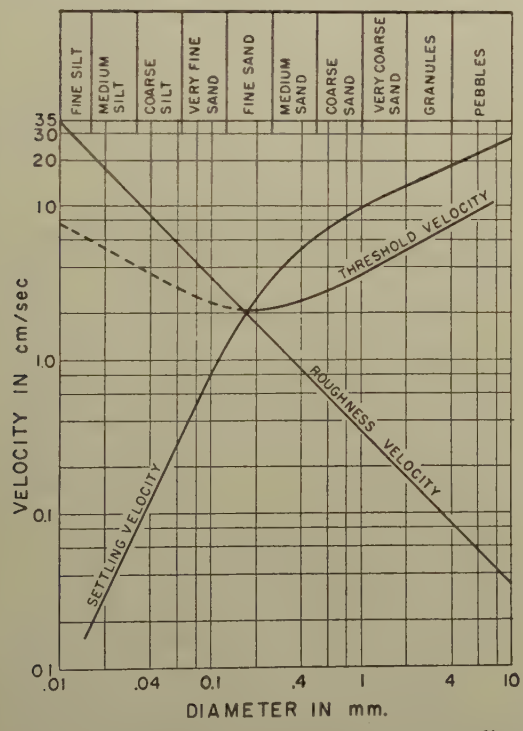


FIG. 5. Relation of grain diameter to settling velocity, threshold velocity, and roughness velocity. Modified from Inman (1949).

equally rather than on exposed individual particles. It is a point of some interest that the roughness velocity, settling velocity, and threshold velocity are the same for grains of 0.18. Thus sand grains of this size are most easily moved.

Since both finer and coarser sediments are more difficult to move, bottom sediments in the act of transport become better sorted as the diameter approaches 0.18 mm. This has been observed in the sediment studies for Cape Cod Bay (Hough 1942), Barataria Bay (Krumbein and Aberdeen 1937), and the Red Sea (Shakri and Higazy 1944).

The sediment analyses in Buzzards Bay agree with the above findings. By far the best sorted sample, Station P, had a median grain size that was precisely 0.18 mm (see Table 2). This station supports the largest total population and the largest number of filter-feeders. The probability is small that this is mere chance. This observation finds further support in the fact that the next largest number of filter-feeders were present at Station N where the sediment was relatively well sorted and median grain size of 0.26 deviated less from 0.18 mm than at any of the other stations. It therefore appears that two sediment criteria, a median grain size in the fine sands and a well-sorted sample, may be correlated with large populations of infaunal filter-feeders.

The Long Island Sound sediment data were reinterpreted from this point of view. These samples as a rule were much more poorly sorted than the Buzzards Bay series. The Charles Island sample of October 23, 1953, had a much larger population of filter-feeders than any of the other stations from which complete sediment analyses could be obtained. Within Long Island Sound the sediment at this station was the best sorted and had a median grain size of 0.15 mm. Thus the Long Island Sound data confirm the Buzzards Bay observations.

Since these results indicate a possible relationship between infaunal filter-feeders and a well-sorted, fine grain, it is pertinent to define the characteristics of such an environment. Because these sediment particles are precisely the sizes most easily

moved, their presence in large concentrations is indicative of little active sediment transport. Such an environment is stable, which is an obvious advantage to organisms that live on and in the sediments.

As particle sizes become larger than 0.18 mm, the material will slide or roll over the bottom rather than go into suspension, because the roughness velocity is less than the threshold and settling velocities (see Fig. 5). Infaunal filter-feeders must maintain connection with the sediment surface in order to feed, and the shifting of the sand particles tend to make the maintenance of this connection precarious. The stations that best typify these conditions in Buzzards Bay (A and E) support very modest populations of infaunal filter-feeders.

Sediments that predominantly consist of silts and clays support meager numbers of filter-feeders for an entirely different reason. These sediments reflect the feeble currents present which allow the fine particles, including the organic matter, to settle out. There is therefore a smaller amount of organic matter in suspension to supply food for the filter-feeders. Most of the stations with fine sediments (Q, O, R, M, F, L and K) support small populations of filter-feeders.

What can be deduced about the well-sorted fine sands? For reasons previously stated, it must be a stable environment. Furthermore, the extremely good sorting indicates that the intensity of the current over the bottom during a tidal cycle must be remarkably constant, probably deviating only slightly from a velocity of two centimeters per second. Finally, currents of this intensity must be adequate to support the large populations of filter-feeders found in such sediments.

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# Some Limnological Features of a Shallow Saline Meromictic Lake

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ABSTRACT

Seasonal variations of some physical, chemical, and biological features were studied from December 1954 to October 1956 in Hot Lake, a shallow saline body of water occupying a former epsom salt excavation in north central Washington. The lake is meromictic and during the period of study had an average salt gradient of approximately 100 g/liter at the surface to 400 g/liter at the bottom, the major salt being magnesium sulfate. The mixolimnion was thin enough that the monimolimnion was heated directly by the sun, with the result that temperatures in excess of 50°C were recorded in the monimolimnion during summer. Much of this heat was retained during the winter. The calculated value of heat gain in the monimolimnion agreed reasonably well with the observed value. The flora consisted mainly of *Chara*, a bottom mat of blue-green algae, and a dense population of green sulfur bacteria in the upper part of the monimolimnion. *Artemia salina* was the dominant zooplankter, and some features of its life history as affected by the unusual thermal properties of the lake are described.

## INTRODUCTION

The purpose of this paper is to report some physical, chemical, and biological features of an unusual meromictic saline lake located near Oroville in north central Washington. The region is semi-arid and has a moisture index value of −20 (Thornthwaite 1948). The paper is a contribution from a project directed by Dr. W. T. Edmondson, on Limnology of Arid Lands, currently being carried out at this institution under the sponsorship of the State of Washington Research Fund in Biology and Medicine and the National Science Foundation. Although the major portion of the project has been concerned with lakes in a somewhat more arid region, the Columbia Basin, the present lake was included in the investigation because of its unusual qualities.

There have been two separate investigations of Hot Lake in the past. St. John and Courtney (1924) investigated the flora of the lake and drainage region but confined their studies to the vascular plants. Only one species of vascular plant inhabited the lake, *Distichlis spicata* (L.) Greene.

Jenkins (1918) described the geology of the region and advanced an explanation for the origin of salts in the lake. The lake bed lies close to rock consisting of metamorphic rocks, dolomites, and shales, and in the drainage area surrounding the lake are numerous mineral deposits consisting mostly of pyrite and pyrrhotite bodies which were largely oxidized to a mixture of iron oxides, quartz, clay, and gypsum. Whitish drainage streaks led from the deposits to the lake, and from this evidence Jenkins postulated the following:

"These facts suggest the possibility that the sulphates and sulphuric acid, known to form from the oxidation of pyrite and pyrrhotite through the action of meteoric water and air, acted upon the dolomite and other magnesian rocks, forming magnesium sulphate, which is soluble, and calcium sulphate, which is much less soluble. The result was that the magnesium sulphate was carried to the lake in solution. What little calcium sulphate came with it was precipitated first, being less soluble, as a thin layer of gypsum over the sediment already deposited on the bottom of the lake."

The dominant mineral, epsomite ($MgSO_4 \cdot 7H_2O$), was in great enough quantity that during and for a short time after the first World War, epsom salt mining operations took place in the lake. These operations revealed a solid 15-foot layer of epsomite beneath the lake bottom. Between the layer of epsomite and bed

rock was a thin layer of gypsum ($CaSO_4$) followed by a thin layer of clay-like material. The morphometry of the lake was changed somewhat by the mining activities which gave rise to the channeled depression now present.

The stimulus for beginning the present investigation was provided by Dr. Phil Church of the University of Washington, Department of Meteorology, who, after a trip to the Oroville area, returned with a water sample and local reports of unusually high temperatures at subsurface depths of the lake. A trip was immediately made to the region, and periodic samplings took place from December 1954 to December 1955, and infrequently during 1956. It is a pleasure to acknowledge the cooperation and courtesies extended by W. Ripley and H. Payne, the owners of the lake, and the Oroville Chamber of Commerce, especially Messrs. C. Wilder and Stafford Lewis. The helpful criticisms and advice of Dr. W. T. Edmondson, University of Washington, in the planning of field work and the assembly and interpretation of the data are particularly acknowledged. Thanks are also due the following people for generous assistance in various ways: Dr. Franz Ruttner, Lunz Biological Station, references to the Hungarian lake studies; Dr. W. T. Edmondson, identification of rotifers; Dr. Francis Drouet, Chicago Museum of Natural History, identification of blue-green algae; Dr. Ralph W. Dexter, Kent State University, identification of the brine-shrimp; U. S. Bureau of Reclamation, Ephrata, Washington, mineral analyses of lake waters.

## MATERIALS AND METHODS

The outline of the shore of Hot Lake was obtained from aerial photographs, and depth contours were added after measurements were made with a brass sounding chain. The sounding program was carried out during maximum water elevation in 1955, and records of seasonal fluctuations were kept.

For the most part, routine sampling was done at a single station in the approximate mid-point of the lake which is also located at maximum depth. Water samples were taken with a Kemmerer water sampler and transported to the laboratory. Analyses included pH (Beckman pH meter), alkalinity titrations with 0.02N $H_2SO_4$ (American Public Health Association 1946), and total dissolved solids. Samples for oxygen determination were fixed in the field and titrated in the laboratory according to the unmodified Winkler method.

Temperature was measured with a direct reading Whitney resistance thermometer. Dr. L. V. Whitney kindly reconstructed the apparatus so that the high temperatures encountered could be recorded. Transparency was measured with a Secchi disc, and light penetration with a Clarke-type apparatus as recommended by the International Council for the Exploration of the Sea (Atkins *et al.* 1938).

The Clarke-Bumpus plankton sampler was used in sampling the zooplankton population, and a № 10 bolting silk net was used throughout. The sampler was towed by rowing at maximum speed as it was impracticable to use an outboard motor due to the small size of the lake. The samples were preserved in formalin and later counted in a plastic tray. When samples were large, aliquots were taken with a wide-mouthed pipette and counted. Otherwise, the entire sample was counted.

## LIMNOLOGICAL NATURE OF THE LAKE

Hot Lake lies in a glacial, wind-protected depression atop Kruger mountain (48°58′N, 119°29′W), part of a low mountain range bordering the Okanogan Valley of north central Washington. The elevation is approximately 2000 feet. Morphometric features include an area of 1.27 ha, maximum depth 3.25 m, mean depth 1.06 m, a channeled depression running most of the length of the lake, and the absence of an inlet or outlet (Fig. 1, Table 1). Investigations have failed to reveal any subsurface flow to the lake. Hence the only apparent source of water is from surface runoff which occurs mainly in early spring. Water loss occurs only by evaporation, and as a result the lake has become extremely saline. Wide variations in surface level and salinity occur

TABLE 1. *Area and volume at different depths in Hot Lake*
Values computed at time when surface level of lake was at the seasonal maximum, May 17, 1955.

| Depth m | Area m² | Volume m³ |
|---|---|---|
| 0 | 12,720 | |
| | | 7940 |
| 1 | 3,982 | |
| | | 3369 |
| 2 | 2,792 | |
| | | 2093 |
| 3 | 1,465 | |
| | | 122 |
| 3.5 | | |
| Total Volume | | 13,524 |

depending upon rates of inflow and evaporation.

Apparently after the lake was re-flooded after mining operations in the early part of the century, a highly saline body of water resulted. As fresh water entered from surface runoff, the lake became stratified and meromixis was established. Because of the protection from the wind, the steep gradient in salinity from top to bottom, and the small surface area, there is a very stable stratification of the monimolimnion. It is not known if the lake was meromictic previous to mining operations or if this condition has been due to the basins formed by the mining establishment.

The nature of meromixis is somewhat different from that generally known in that separation into mixolimnion and monimolimnion is not distinct. Rather, there is at most times a sharp gradient in density from top to bottom with the gradient being somewhat more abrupt (chemocline) at the middle level of the lake. The major difference from meromictic lakes previously described is in the structure of the upper layer or mixolimnion. Most meromictic lakes (Findenegg 1935, Hutchinson 1937, Anderson 1958) have mixolimnia of uniform density throughout and are freely circulating except during times of temperature stratification. In Hot Lake that portion of the water mass which can best be described as the mixolimnion is at most times stratified due to differences in salt concentration, and wide seasonal variation

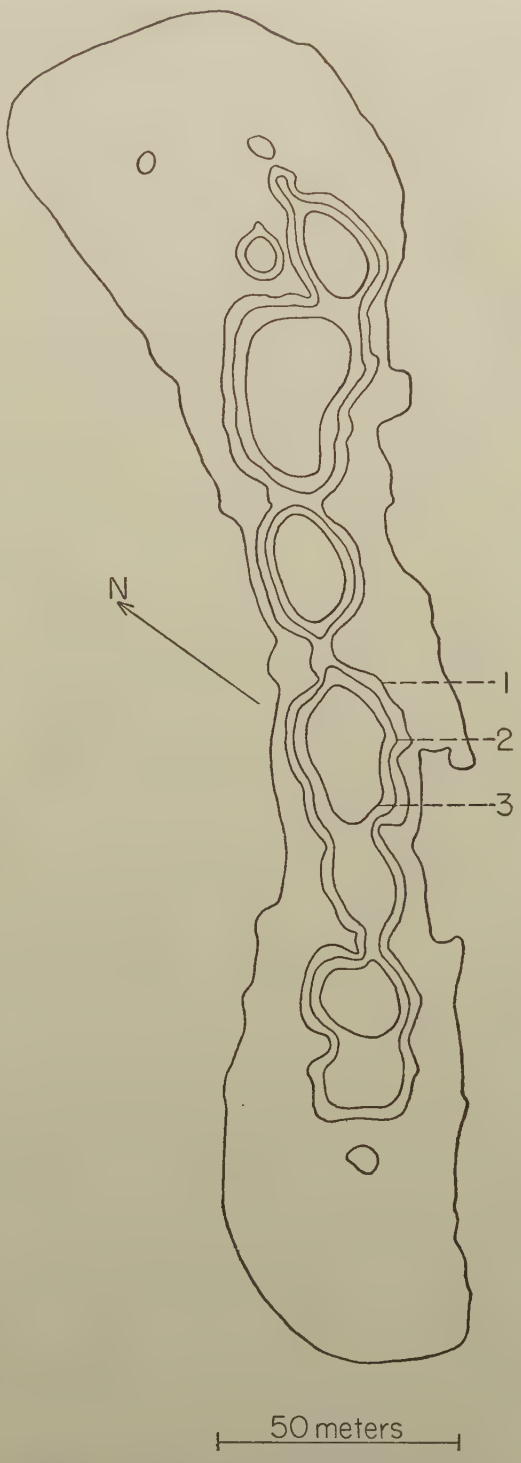


FIG. 1. Bathymetric map of Hot Lake, Washington, with depth contours in meters.

in characteristics occur. This is especially evident during the spring season after the lake has gained considerable fresh water from runoff. At this time the upper water, as distinct from the monimolimnion, is a two-layered stratum, the top layer of which is relatively fresh. Due to the marked wind protection mixing takes place slowly, and gradually the two-layered upper stratum loses its identity. As a result a mass of water with a density gradient from surface to the top of the monimolimnion is established, which in this paper is referred to as the mixolimnion. Because of mixing, evaporation, and addition of water each spring, the surface waters are subject to great changes in salt content with the trend being that of increase from spring to fall.

The problem of maintenance of meromixis is an interesting one. It might appear that stratification would break down eventually in meromictic lakes with a small volume and depth such as Hot Lake because of diffusion and other mixing processes. However, it must be remembered that not only is mixing kept at a minimum by protection from wind, but also the addition of a stratum of fresh water to the lake by spring runoff each year adds to the stability. In addition, and probably a most important factor, salt solutions in freezing precipitate a portion of their dissolved materials (Thompson and Nelson 1956). In this manner, seasonal losses of salt from the monimolimnion due to diffusion into the mixolimnion could be renewed during the winter period of ice cover.

## PHYSICAL CONDITIONS

### *Temperature*

The type of temperature stratification found in Hot Lake is unusual (Table 2). The temperature profile shown in Figure 2 (May 17, 1955) is typical of summer thermal conditions. Temperature at the surface was approximately 18°C and increased sharply with depth to the 1.5-m zone. A middle region, 1.5–2.2 m, represented a layer of maximum temperature (40°C), and from this region to the bottom the temperature decreased steadily to slightly less than 29°C.

TABLE 2. *Seasonal and vertical variation of temperature (°C) and seasonal variation of transparency (m) in Hot Lake, December 1954 to October 1956*

| | 1954 | 1955 | | | | | | | | | | | | | 1956 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Depth (m) | Dec. 7 | Mar. 12 | Apr. 16 | May 17 4:30 a.m. | May 17 12:40 p.m. | May 17 4:25 a.m. | May 18 5:25 a.m. | May 29 | June 25 | Jul. 23 | Aug. 22 | Sept. 28 | Oct. 18 | Dec. 9 | May 1 | May 18 | Oct. 24 |
| 0.0 | Ice | Ice | 14.40 | 11.00 | 17.92 | 17.53 | 13.29 | 20.31 | 21.00 | 26.77 | 21.92 | 13.73 | 11.70 | Ice | 13.61 | 23.12 | 6.48 |
| 0.25 | | | | | | | | | | | | | | | 13.66 | 22.48 | |
| 0.5 | | 2.20 | 18.90 | 25.55 | 26.95 | 27.14 | 26.40 | 22.61 | 20.29 | 26.38 | 21.83 | 13.54 | 11.57 | 0.00 | 13.67 | 26.80 | 8.10 |
| 0.75 | 5.20 | | | | | | | | | | | | | | 24.58 | 31.81 | 18.45 |
| 1.0 | 6.00 | 4.85 | 23.60 | 31.25 | 31.90 | 32.00 | 31.40 | 36.20 | 26.10 | 28.43 | 21.58 | 13.39 | 11.47 | 0.00 | 25.90 | 34.37 | 25.17 |
| 1.25 | | | | | | | | | | | | | | | 20.42 | 28.98 | |
| 1.5 | 16.00 | 11.18 | 27.50 | 37.20 | 38.10 | 39.70 | 39.20 | 44.50 | 45.75 | 42.68 | 32.17 | 13.70 | 11.47 | 0.00 | 16.45 | 22.21 | 29.48 |
| 1.75 | | | | | | | | | | | | | | | 12.60 | 17.62 | |
| 2.0 | 23.80 | 18.85 | 30.30 | 38.90 | 40.00 | 41.10 | 40.30 | 45.30 | 49.72 | 50.53 | 43.65 | 27.64 | 21.38 | 8.00 | 10.25 | 13.99 | 27.18 |
| 2.25 | | 20.61 | | | | | | | | | | | | | 8.29 | 11.39 | |
| 2.3 | | 21.10 | | | | | | | | | | | | | | | |
| 2.5 | 29.00 | | 28.60 | 35.30 | 35.30 | 35.60 | 35.60 | 37.84 | 42.38 | 43.88 | 40.93 | 33.36 | 27.43 | 16.48 | 7.49 | 10.22 | 23.52 |
| 2.75 | | | | | | | | | | | | 33.85 | 29.73 | 20.00 | 6.67 | 9.03 | |
| 3.0 | | | 26.90 | 31.80 | 31.72 | 31.70 | 31.67 | 32.05 | 34.65 | 36.19 | 36.67 | | | | 6.83 | 8.63 | 20.70 |
| 3.1 | | | | | | | | | | 35.68 | 35.72 | | | | | | |
| 3.2 | | | | | | 29.90 | | | 32.88 | | | | | | | | |
| 3.25 | | | 26.90 | 28.30 | 28.71 | | | 29.70 | | | | | | | 7.48 | 8.82 | |
| 3.3 | | | | | | | 29.09 | | | | | | | | | | |
| 3.5 | | | | | | 28.78 | | | | | | | | | 8.33 | 9.30 | 18.20 |
| 3.75 | | | | | | | | | | | | | | | 9.98 | 10.32 | |
| 4.0 | | | | | | | | | | | | | | | 10.60 | | |
| Transparency | | 2.0 | 2.3 | | | | 2.2 | | 2.0 | 2.0 | 1.8 | 1.7 | 1.3 | | 1 | 1.1 | 1.3 |

The water to a depth of 2 m is clear, whereas the monimolimnion is characterized by a dark brown, stagnant water containing hydrogen sulfide. Slightly below the 2-m level a thin layer of opaque green colored water was present. This was due to a large population of what appeared to be green sulfur bacteria, possibly *Chlorobium*. Light is readily transmitted through the transparent mixolimnion, but is absorbed rapidly in the bacterial zone and darkly colored monimolimnion. The heat gained in the monimolimnion from absorption of light energy cannot readily escape because of lack of circulation between the upper and lower layers. The mixolimnion, on the other hand, can gain a greater amount of heat from light energy and from atmospheric transfer on warm days, but can also lose this heat rapidly during periods of low atmospheric temperature such as during nights and during the cold season. Apparently, the major means of escape of heat from the monimolimnion is by conduction to the bottom and to the mixolimnion, but this is a slow process, as is evidenced by the gradual loss of heat during the period December 1954 to March 1955 (Fig. 3).

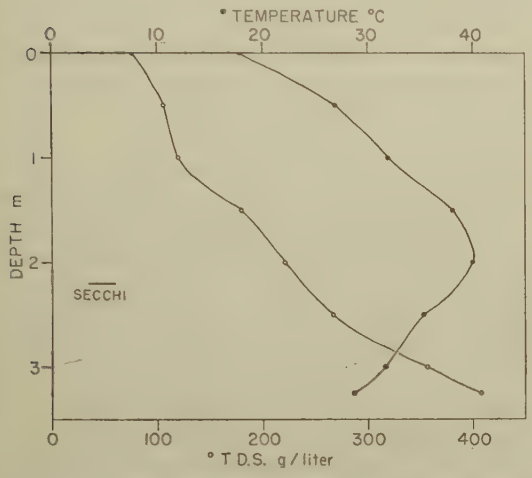


FIG. 2. Vertical distribution of temperature and salt concentration in Hot Lake, May 17, 1955.

Other bodies of water with similar therma

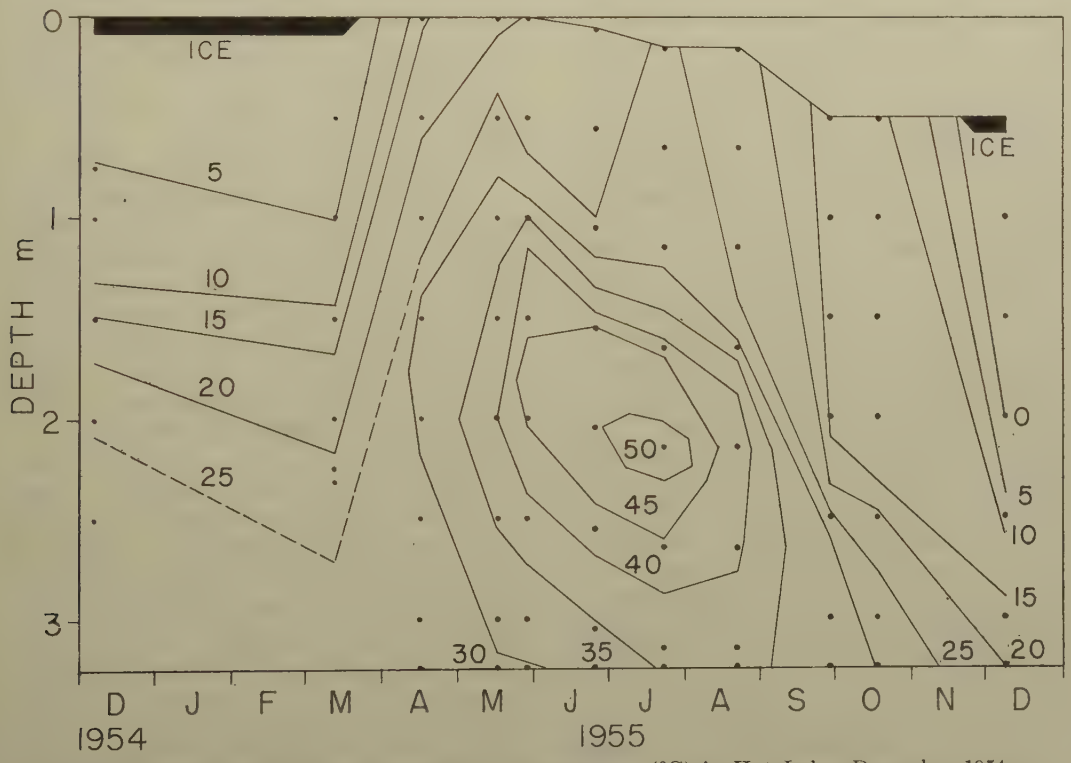


FIG. 3. Seasonal and vertical variations of temperature (°C) in Hot Lake, December 1954 to December 1955.

characteristics have been reported in the literature. Beadle (1943) reported similar small bodies of water in Algeria, the most striking being 0.3 m deep with a specific gravity of 1033 at the top and 1172 at the bottom. The surface temperature was 19.0°C and the bottom temperature 31.0°C. Kalecsinsky (1901) reported on some saline wind-protected lakes in Hungary which were overlain by shallow sheets of fresh water. The major part of his study was concerned with Medve See, which had a concentration of 24 per cent sodium chloride, a depth of 20 m, and an area of 4.3 ha. He found a maximum temperature of 56.0°C at 1.32 m, but earlier workers had found temperatures up to 71.0°C at depths below the surface. Schafarzik (1908), in a later study, reported a maximum temperature of 45.6°C at 2.0 m in Medve See, and Halbfass (1923) reports still another study of the same lake in which the maximum temperature occurred at 2.5 m. Since none of the lakes studied had a hot spring source and the rise in temperature was too great to explain by chemical oxidation of organic materials, the several investigators concluded that the radiant energy of the sun was stored in the saline waters immediately below the upper less concentrated zone, since release of heat is not possible due to lack of circulation. Similar thermal characteristics are also found in some oyster polls on the west coast of Norway (Gaarder and Spärck 1932). These polls are located in fjords which are connected to the open ocean by narrow and shallow entrances. Temperatures up to 28.0°C were recorded at subsurface depths after rain water had covered the surface during spring.

On December 7, 1954, the first sampling date, the lake had just frozen over and had less than 1 cm of ice cover. There was an almost uniform gradient in temperature with a maximum of 33°C at the bottom (Fig. 3). The next sampling data, March 12, 1955, after a winter of heavy ice cover, was at a time just before the ice left the lake. About 13 cm of slushy ice remained on the surface. Some heat had been lost from the monimolimnion, and the maximum temperature observed at the bottom of this stratum was 21°C. A steeper temperature gradient between 1.5 and 2.0 m was noted which indicated a discontinuity layer at the same level as shown by measurements of total dissolved salt. The lake gained heat rapidly after the disappearance of ice, and by April 16 the temperature profile had changed considerably. The maximum gain of heat occurred at the 2 m level. The surface temperature was 14°C, at 2 m 30°C, and a slight decrease to 27°C was noted at the bottom.

During most of the summer the gain in heat of the lake followed the same trend. The surface temperature reached a maximum of 27°C, the same magnitude as would be expected in most lakes of comparable size in the region. However, the temperature of the water in the 2 m region rose steadily and was always higher than that of the surface or the bottom. The bottom waters showed a steady gain during the summer, but the magnitude was small in comparison with the surface and middle waters.

The observed date of maximum heat was July 23, 1955. The series taken August 22, 1955, showed an overall loss of heat. The surface temperature had decreased to 21.7°C and the 2 m level to 43.6°C. The bottom waters remained relatively constant in temperature.

There are three factors which contributed to the loss of heat during August. The first factor is the lessening of solar energy input as the days became progressively shorter. The second factor, reduction in the thickness of the mixolimnion due to evaporation, decreased the insulation protecting the middle layer of maximum heat. Thus, the process of conduction of heat from the middle depth of the lake to the surface could occur over a shorter distance and become of greater significance. Also, disturbances in the upper water from wind would then more readily affect the lower waters by mixing. During the summer a health resort was established near the lake, and pumping of sub-surface waters for hot baths took place. Because figures are not available on the amount of water removed, it is not known if pumping contributed significantly to the loss of heat noted.

The lake lost heat rapidly during the fall

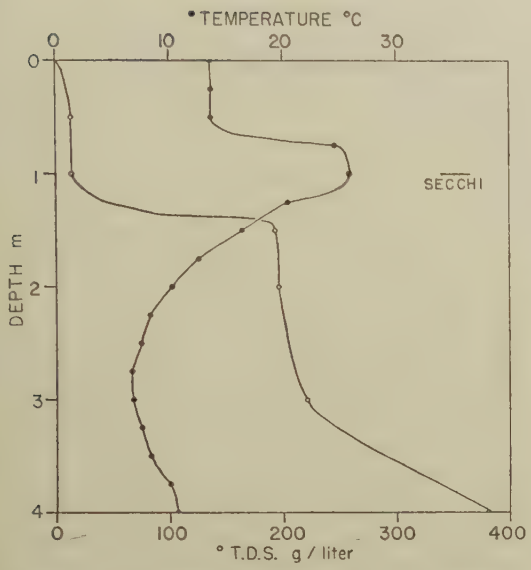


FIG. 4. Vertical distribution of temperature and salt concentration in Hot Lake, May 1, 1956.

and winter of 1955–56. The amount of heat retained in the preceding winter was much greater, which was presumably due to a lesser amount of mixing in that winter. In December 1955, the lake level was 0.5 m lower than in December 1954, and mixing, as indicated by temperature measurements, extended to approximately 0.5 m in 1954 and 1.5 m in 1955.

In 1956 the lake received more than 1 m of fresh water on the surface from heavy snowfall during the preceding winter. Only three series of measurements were taken during this year, but it is interesting to compare thermal conditions with 1955 (Table 2, Fig. 4). On May 1, 1956, the mixolimnion was nearly uniform in salinity to a depth of 1.0 m. The average transparency was 1.0 m. In accordance with these measurements, the region of maximum temperature was at 1.0 m in 1956, whereas in 1955 transparency was usually about 2.0 m, the depth of maximum heat. In both years the mixolimnion was relatively transparent, and directly beneath it a layer of highly colored water occurred, which accounted for the increase in temperature due to light absorption. Another feature of conditions in 1956 was the presence of a layer of water directly on the bottom which was warmer than that immediately above it. This apparently represents that portion of the lake which had remained relatively undisturbed since 1955.

### *Transparency*

Transparency as indicated by Secchi disc observations varied with the depth of the mixolimnion (Table 2). Waters of the mixolimnion were of a clear relatively colorless nature, whereas the monimolimnion was highly colored. The Secchi disc could at any time be seen clearly at any depth in the upper water, but after entrance into the monimolimnion immediately disappeared from sight. By autumn of 1955, after considerable evaporation and mixing had occurred, the upper water became slightly colored, presumably due to the intrusion of the colored monimolimnion water. In 1955 the maximum value was 2.3 m in April, the minimum value 1.3 m in October. Transparency in 1956 was reduced, with a maximum of 1.3 m in October and a minimum of 1.0 m in May.

### *Light penetration and heating*

Because of the unusual thermal properties of Hot Lake it seemed advisable to acquire information on the penetration of different wavelengths of light and to relate the absorption of light to heating at different depths. On August 23, 1955, measurements of light penetration were made in the visible spectrum (3800–7200 Å), roughly the range of the photoelectric cell used (2700–7500 Å). Measurement of ultra-violet and infra-red was not possible with the available equipment, but it is known that both components are absorbed rapidly by pure water and their effect on subsurface water is negligible (Clarke 1939). The five wavelengths investigated were 4500, 5250, 5750, 6150, and 6800 Å. Their transmission is illustrated on a semi-logarithmic scale as percentages of illumination measured just beneath the surface (Fig. 5). Maximum transmission occurred in the yellow region, and absorption at each end of the visible spectrum was great.

With the data at hand it is possible to compute the amount of heat the lake could gain at a given depth. Light was trans-

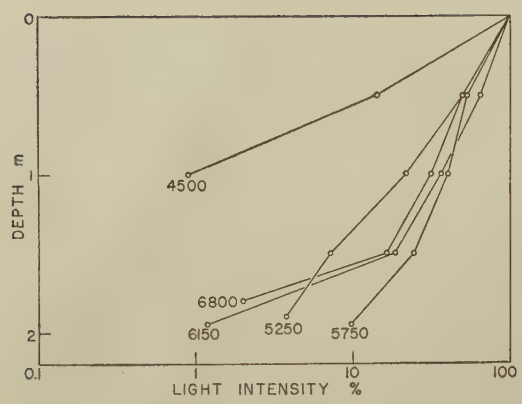


Fig. 5. Intensity of different wavelengths of light (Å) in the visible spectrum at various depths in Hot Lake, August 23, 1955.

mitted through the upper water fairly readily, but at 1.8 m there was a sharp break, beyond which light was scarcely measurable due to the beginning of the highly colored monimolimnion. The calculated intensity of light at 1.8 m was 3.62 per cent of surface illumination, and for purposes of the present discussion it is assumed that complete absorption occurred in the 10-cm depth zone directly below 1.8 m. If an average summer value of 600 g-cal/cm²/day is arbitrarily assigned as the amount of light energy falling on the lake surface, then 21.72 g-cal/cm² would reach 1.8 m in one day and would be completely absorbed within the next 10 cm. This would allow the average temperature of that zone to rise 2.17°C/day if it were pure water. However, a 25 per cent solution of $MgSO_4$ at 25°C has a specific heat of 0.743 (National Research Council 1928) which would increase the above value to 2.92°C/day.

On May 17 and 18, 1955, the actual amount of heat gained in the lake at different depths was measured (Table 3). Vertical temperature series were taken at dawn and late afternoon on the first day and at dawn on the following day. In this manner the heat gain in daylight hours and the net gain in a 24-hour period was measured. The heat gain from 4:30 a.m. to 4:25 p.m. was considerable and occurred only above 2.5 m. Apart from the surface, the heat gain was the greatest in intermediate waters (1.5–2.0 m). At 2.0 m the gain was 2.20°C, which is in reasonably close agreement with the computed value of 2.92°C at 1.8–1.9 m in view of the assumptions necessarily made. Since the heat gained in the intermediate waters would not be expected to be completely retained due to conduction and other mixing processes, a lower actual value than that calculated seems reasonable. This is evidenced by the heat loss of 0.80°C at 2.0 m during the night, leaving a net gain of 1.40°C/day.

Table 3. *Diurnal temperature variations at different depths in Hot Lake, May 17 and 18, 1955 (°C)*

| Depth m | May 17 4:30 a.m. | May 17 4:25 p.m. | Heat gain | May18 5:25 a.m. | Heat loss | Net gain |
|---|---|---|---|---|---|---|
| 0 | 11.00 | 17.53 | 6.53 | 13.29 | 4.24 | 2.29 |
| 1 | 31.25 | 32.00 | 0.75 | 31.40 | 0.60 | 0.15 |
| 2 | 38.90 | 41.10 | 2.20 | 40.30 | 0.80 | 1.40 |
| 3 | 31.80 | 31.70 | −0.10 | 31.70 | 0.00 | −0.10 |

## CHEMICAL CONDITIONS

As stated previously, the lake contains predominantly the mineral, magnesium sulfate (Table 4). Other ions are present, the most conspicuous being chloride, bicarbonate, and sodium. Qualitatively the mixolimnion and monimolimnion were similar, although the latter was characterized by having a much greater salt content and a noticeable amount of $H_2S$ as revealed by the strong odor.

Large fluctuations occurred in salt concentration of surface waters. After the spring runoff in 1955 a minimum of 40 g/liter was recorded (April 16), and by late summer, evaporation and mixing accounted for an increase to a maximum value of almost 200 g/liter. A typical profile of salt distribution in 1955 is shown in Figure 2. In 1956 the runoff was great, and as a result the surface waters contained relatively little dissolved materials (0.37 g/liter) (Fig. 4).

The pH was generally alkaline. The maximum was 8.72 at the surface on December 7, 1954, and the minimum was 6.98 at the bottom on the same date.

TABLE 4. *Mineral analyses of Hot Lake waters, August 22, 1955*
Ion concentration expressed as mg/liter, conductivity as micromhos at 25°C. Analysis by Bureau of Reclamation, Engineering Laboratories Branch, Denver, Colorado.

| | Surface | 3 m |
|---|---|---|
| Conductivity | 57,910 | 60,440 |
| pH | 8.2 | 7.8 |
| T.D.S. | 161,200 | 391,800 |
| Ca | 640 | 720 |
| Mg | 22,838 | 53,619 |
| Na | 7,337 | 16,790 |
| K | 891 | 1,564 |
| $HCO_3$ | 3,148 | 3,062 |
| $CO_3$ | 0 | 0 |
| $SO_4$ | 103,680 | 243,552 |
| Cl | 1,668 | 1,882 |
| $NO_3$ | 0 | 0 |

There was usually an abundance of dissolved oxygen in the surface waters (maximum 12.9 mg $O_2$/liter, April 10, 1955) except in the autumn of 1955 when none was detectable. Oxygen was never found below 1.5 m. Because of the abundance of $H_2S$ in the monimolimnion and probable diffusion of it into the mixolimnion, especially during the period of low lake level, the unmodified Winkler method is probably not suitable, and the information obtained thereby should be viewed with some scepticism. It is possible that oxygen extended somewhat below 1.5 m at times, but because of increasing $H_2S$ interference with depth, apparent zero values could be encountered in depths shallower than the actual zero point. $H_2S$ interference must surely be the explanation for the apparent zero value recorded in surface waters during autumn 1955, judging by the presence of *Artemia* in these waters.

## BIOLOGICAL CONDITIONS

### *Flora*

Two conspicuous constituents made up the bottom dwelling flora. *Chara* sp. was abundant in the shallow waters around shore, and beginning at a depth of approximately 1.0 m there was a thick mat of blue-green algae. The mat was made up of four species: *Plectonema nostocorum* Gom., *Oscillatoria chlorina* Gom., *Anacystis thermalis* (Menegh.) Drouet & Dailey, and *Gomphosphaeria aponina* Kuetz. Dr. Francis Drouet commented that these forms are sometimes found in hot springs but are not the common species of such habitats. However, they belong to a limited group of blue-green algae, which not only survive but grow vigorously in a wide range of environmental and physiological conditions. Evidence of this is seen in Hot Lake where the mat extends into the lower regions of the anaerobic monimolimnion, a factor which suggests hydrogen sulfide metabolism.

The presence of a rich population of green sulfur bacteria, possibly *Chlorobium*, was mentioned previously. The population was found in the upper part of the monimolimnion, slightly below 2.0 m. Its influence upon the absorption of light and resultant heating of the surrounding water has been discussed.

### *Fauna*

The zooplankton in 1954 and 1955 consisted predominantly of the brine-shrimp, *Artemia salina* (Linnaeus). The rotifer, *Brachionus angularis* Gosse, was the only other zooplankter of note, but there were also occasional records of the rotifer *Keratella quadrata* (Müller), calanoid and cyclopoid copepods, and an ostracod.

Some features of the seasonal life history of *Artemia* are apparent from investigation of the fluctuations in numbers of eggs floating free in the water, immature forms, and adults (Fig. 6). Events occurring during the winter are not clear because few samples were collected then. Adult and immature forms were found in December of 1954 accompanied by relatively large numbers of free-floating eggs. Just prior to the disappearance of ice on the lake in March a large population of immature stages had developed, but there was little change in the populations of adults and eggs. The peak population of adults which occurred in July was accompanied by the maximum number of eggs. Shortly after this time the adult and egg numbers dropped, but a resurgence of immature forms occurred, probably due to reproduction of adults from the prior maximum. By Oc-

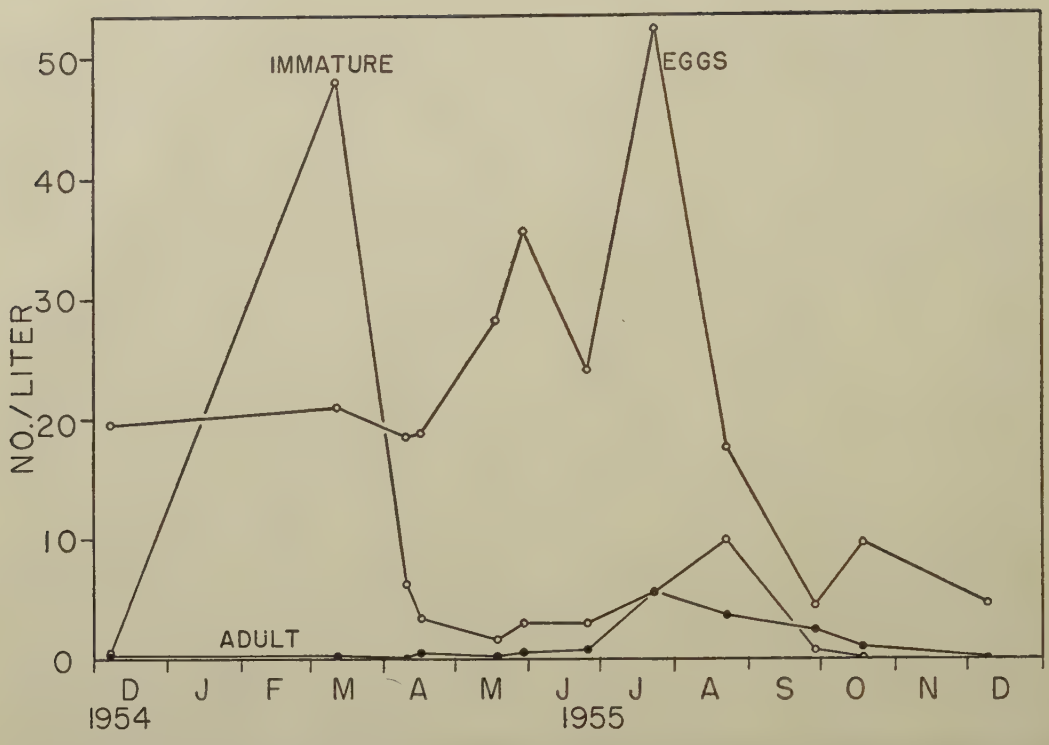


FIG. 6. Seasonal fluctuations of the egg, immature, and adult populations of *Artemia salina* in Hot Lake, December 1954 to December 1955.

tober the total population had dropped to low numbers, and in December only a few free-floating eggs were found.

The large crop of immature stages present in March, 1955, was apparently not successful, because it would be expected that under favorable conditions a large crop of adults soon would have resulted, assuming that the adult stage is long lived relative to the period of immaturity. The lake still had a fairly heavy ice cover at this time, and it may have been that the zone between the upper cold water and the lower warmer anaerobic zone was too restricted for such a large population.

It has been observed at times that *Artemia* shows a preference for certain depths of the lake at different times of the year. In December 1954 and early spring of 1955, it was noted from visual observations that the major portion of the population gathered in the lower reaches of the mixolimnion, presumably due to a temperature preference for the lower warmer waters. As summer progressed the population migrated to the surface waters. Apparently *Artemia* was excluded from the lower part of the mixolimnion after the temperature rose above 30°C. Because of the presence of warm and presumably oxygenated waters in some part of the mixolimnion during the winter of 1954–55, it was possible for reproduction to occur throughout most of the year. Copulating pairs were found on all sampling dates except December 9, 1955. It was reported in the discussion of temperature variation in the lake that the mixolimnion was much reduced in volume by evaporation throughout the latter part of 1955, and that by the time of ice cover in the winter the temperature of the entire mixolimnion had been reduced to slightly below 0°C, thus eliminating chances of survival of the adult population.

In 1956 conditions were different, but due to the infrequency of sampling, seasonal events cannot be described. However, there was one observation worthy of note. Much of the water added to the lake from melting snow remained relatively fresh and sup-

ported a large population of an undescribed species of *Branchinecta* (Dr. James E. Lynch, University of Washington, personal communication). *Artemia* inhabited the original upper layer of the lake, immediately beneath the "fresh" zone. The green sulfur bacteria were again found in the upper region of the monimolimnion. Transparency was such that one could readily see each of these regions with its inhabitants. Apparently *Branchinecta* and *Artemia* were confined to different regions by salinity requirements, whereas anaerobic conditions in the bacterial zone excluded the animals but were necessary for the growth of the bacteria.

## SUMMARY

1. Seasonal variations of some physical, chemical, and biological features were investigated in Hot Lake, a meromictic saline lake occupying a former epsom salt excavation in north central Washington.

2. Because the lake has neither an inlet nor outlet, evaporation is important, and wide variations in salt concentration of the mixolimnion were common. The mixolimnion was never completely isohaline, and during the spring of 1956 a sufficient amount of melt water was received to establish temporarily a three-layered lake.

3. Thermal stratification was marked. The mixolimnion was thin enough that the monimolimnion was heated directly by the sun and developed a persistent high temperature—in excess of 50°C in July 1955. Much of the heat was retained through the winter, with temperatures higher than 20°C recorded in the bottom at the time of ice melt in spring.

4. The mixolimnion was transparent, the monimolimnion opaque. Maximum transmission of light occurred in the yellow region of the spectrum. Absorption of light at the top of the monimolimnion was great enough that the computed amount of heat the lake could gain at this depth from light absorption alone was 2.92°C/day. An observed value was 2.20°C/day.

5. The major mineral in the lake was epsomite ($MgSO_4 \cdot 7H_2O$). The pH was mostly alkaline, dissolved oxygen was never recorded below a depth of 1.5 m, and large quantities of $H_2S$ were present in the monimolimnion.

6. The flora consisted principally of *Chara* sp. and a bottom mat of blue-green algae. Water at the top of the monimolimnion contained a dense population of green sulfur bacteria. The dominant zooplankter, *Artemia salina*, occurred at most times of the year, presumably due to the retention of heat at intermediate levels during winter. Copulating individuals were found at all sampling dates with the exception of the winter of 1955–56 when the temperature of the entire mixolimnion dropped below 0°C and the population disappeared. After the spring runoff in 1956 *Branchinecta* sp. inhabited the upper "fresh" zone, whereas *Artemia* was confined to lower more saline waters.

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# Environmental Factors Involved in Setting the Phases of Tidal Rhythm of Color Change in the Fiddler Crabs *Uca pugilator* and *Uca minax*[1]

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ABSTRACT

Observations were performed to determine the relationship between the time of maximal pigment dispersion in the fiddler crabs, *Uca pugilator* and *Uca minax*, and the tidal events on the beach where the crabs were collected. *Uca pugilator* obtained from burrows above the high tide mark did not have an overt tidal rhythm but did have 24-hour and 14.8-day cycles of color change. The tidal rhythm was probably suppressed because the crabs were free to leave their burrows at any time, whereas crabs from the intertidal zone can leave only when the area where their burrows are located is uncovered by the receding water. Crabs living in the intertidal zone displayed a typical tidal rhythm of color change. The tidal maximum of pigment dispersion progressed across the 24-hour cycle at the usual rate. Analysis of the tidal rhythms of two groups of crabs, *Uca pugilator*, collected near the high and low tide marks, respectively, revealed that crabs from burrows near the low tide mark behaved as if low tide occurred for them 9.8 hours later each day than for the high tide crabs. Crabs living near the low tide mark appeared on the beach 10.1 hours later than crabs living near the high tide mark. As a result of these observations the hypothesis was presented that the phases of the tidal rhythm are set primarily according to the time that the area where the crabs live is uncovered by the receding water, and secondarily according to the time required for the area to drain so that the sand is firm enough to support holes from the burrows to the surface.

A review of the literature concerning tidal and semilunar rhythms of color change has appeared recently (Fingerman 1957a). Brown *et al.* (1953) published the first report of these rhythms. The fiddler crab *Uca pugnax* collected in the region of Woods Hole, Massachusetts, where the tides are semidiurnal, would darken by day and blanch by night in accordance with a 24-hour rhythm of color change. Superimposed upon the latter was a tidal cycle that progressed across the 24-hour rhythm at the average rate of 48.8 minutes per day. The tidal rhythm was evidenced by a supplementary dispersion of pigment in the melanophores about the time of low tide. A semilunar rhythm was also evident from analysis of the data. The frequency of this rhythm was 14.8 days, the average interval between days on which the 24-hour and tidal rhythms repeated similar time relations to one another. More recently, Brown *et al.* (1955) showed that *Uca pugnax* has the endogenous ability to mark off periods of solar and lunar day-lengths in the absence of all possible rhythmic external signals.

Persistent tidal and semilunar rhythms of color change were observed in the blue crab, *Callinectes sapidus*, by Fingerman (1955). These rhythms were similar to those described above for *Uca pugnax* in spite of the fact that the *Callinectes* were collected in the vicinity of New Orleans, Louisiana, a region of diurnal tides. Evidently the "center" of tidal rhythmicity of color change in blue crabs operated on the basis of tides spaced 12.4 hours apart, although the crabs were collected in a region where 24.8 hours was the average interval between successive low tides.

In addition to *Uca pugnax*, tidal rhythms of color change have been observed in *Uca pugilator* and *Uca speciosa* by Fingerman (1956). The latter two species were collected at Ocean Springs, Mississippi, where the tides are diurnal. The tidal rhythms of both species were similar to the tidal rhythms of *Callinectes sapidus* and *Uca pugnax*. Both the *Uca pugilator* and

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*Uca speciosa* were collected from delimited portions of the beach. Analysis of the tidal rhythms of both species revealed that the *Uca speciosa* behaved as if low tide occurred for them 7.5 hours earlier in the day than low tide for the *Uca pugilator*.

Inspection of the beach at Ocean Springs revealed that the area where the *Uca speciosa* were collected was closer to the high tide mark than where the *Uca pugilator* were found. The phase difference between the tidal rhythms was probably due to the fact that when the water receded after high tide, in effect low tide occurred earlier for crabs living near the high tide mark. *Uca speciosa* would, therefore, be free to leave their burrows and feed earlier than the *Uca pugilator* living closer to the actual low tide mark. Measurements of the beach revealed that the water actually uncovered the area where the *Uca pugilator* were found about 4.9 hours after the region of the *Uca speciosa* was uncovered.

In view of the possibility that the phase difference between the tidal rhythms of color change of *Uca pugilator* and *Uca speciosa* was a species difference and not due to the difference in times of uncovering the two burrowing areas, the tidal rhythm of color change of *Uca pugilator* was subjected to further analysis (Fingerman 1957b). A two-day phase difference, equivalent to 1.6 hours in a tidal cycle, was found in the laboratory between two groups of crabs collected from two discrete sets of burrows different distances from the high tide mark. Maximum pigment dispersion at any given hour of the day occurred two days earlier in crabs collected nearer the low tide mark.

Measurements of the beach where the crabs were collected revealed that the receding water uncovered the area closer to the high tide mark about 1.6 hours earlier than the region closer to the low tide mark was uncovered, the same as the phase difference in the tidal rhythms of the two groups that was observed in the laboratory. The time of supplemental pigment dispersion, therefore, appeared to be set each day according to the time the regions where the burrows were located began to be uncovered by the receding water following a high tide and not according to the time of actual low tide on the beach.

The present investigation was undertaken to analyze further the tidal rhythm of color change in fiddler crabs. First of all, the endogenous color changes of fiddler crabs living beyond the high tide mark were determined from day to day and analyzed. Then the concept that the times of supplemental pigment dispersion are set according to the time the burrowing region begins to be uncovered by the receding water following a high tide was subjected to further inquiry. When the phase difference in the tidal cycle of 7.5 hours was observed, crabs from burrows near the high tide mark and from burrows approximately midway between the high and low tide marks were used (Fingerman 1956). However, when the 1.6-hour phase difference was noticed, crabs from the latter set of burrows and from burrows closer to the low tide mark were observed (Fingerman 1957b). In the present investigation fiddler crabs from the burrows near the high tide mark and from those closest to the low tide mark were collected and observed to determine if the phase difference in their tidal rhythms would approximate the sum of the previously determined phase differences of 7.5 and 1.6 hours, namely 9.1 hours.

## MATERIALS AND METHODS

Fiddler crabs, *Uca pugilator* and *Uca minax*, were collected on the beach near the Gulf Coast Research Laboratory, Ocean Springs, Mississippi, for use in the observations reported below. The authors wish to express their gratitude to Dr. Fenner A. Chace, Jr., of the U. S. National Museum who identified the *Uca minax*.

Crabs were collected for the first series of observations on June 11 and 12, 1957, and transported in stainless steel aquaria to an air-conditioned laboratory in New Orleans, Louisiana, where observations were initiated at 8 A.M. on June 13. All hours mentioned are Central Standard Time. From the evening of June 12 until the end of the

period of observation the crabs were maintained in darkness except for the few minutes required to observe the melanophores on days observations were being performed and to change the water in the aquaria on days observations were not performed. The crabs were kept in inclined, covered, stainless steel aquaria containing sufficient sea water to cover approximately one-half the bottom. The crabs were, therefore, free to move in and out of the water. For the second series of observations crabs were collected on June 22 and returned to New Orleans the same day. Observations on these crabs began at 8 A.M. on June 23.

Melanophores were staged in the manner described by Fingerman (1956). The average index was determined for the melanophores on the anterior aspect of a walking leg with the aid of a stereoscopic dissecting microscope and lamp. The chromatophore indices of Hogben and Slome (1931) were used in staging the chromatophores. The most concentrated state of the pigment is referred to as stage 1, the most dispersed stage 5, and the intermediate conditions stages 2, 3, and 4. Fifty crabs could be staged in three minutes. The senior author would call out the indices and a second individual would record the data. The methods of data analysis were those that have been fruitful previously (Brown *et al.* 1953; Fingerman 1955, 1956, 1957b).

## RESULTS

### *Description of the beach*

The dot on the map represents the area where the crabs were collected (Fig. 1). The substrate of most of the intertidal zone was grayish-black mud. Marsh grass covered the upper two-thirds of the zone except for a small sandy area near the high tide mark. This region, approximately 25 feet long parallel to the shore and 15 feet wide, was composed of coarse brown sand. One group of crabs was obtained from this area. The second was obtained from the set of burrows in the mud near the low tide mark. The latter set of burrows was found in a section of beach about 10 feet long parallel to the shore and 7 feet wide.

The beach has a very gradual slope (Fig. 2). In this figure horizontal distance is plotted in meters and elevation in centimeters. This method of plotting was chosen because in 89 meters of beach the rise was

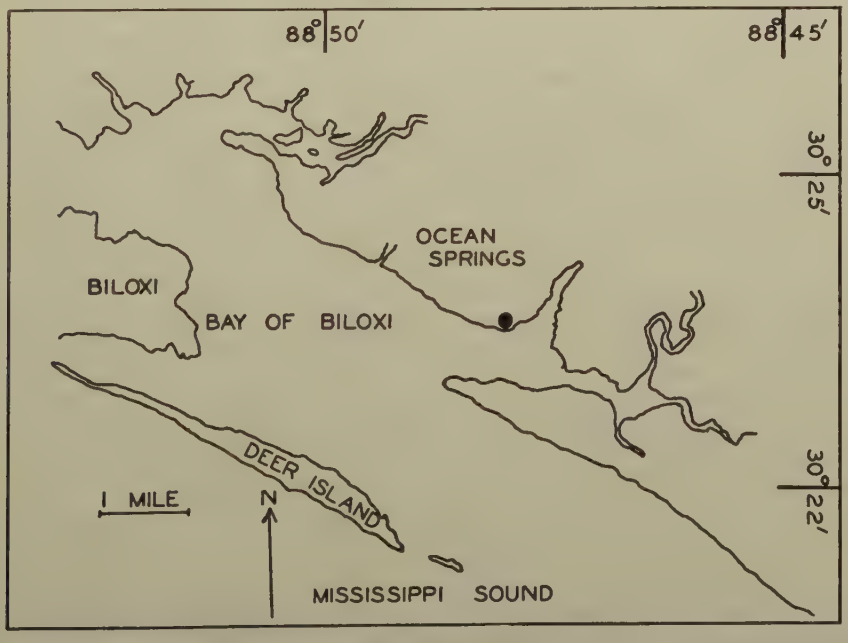


FIG. 1. Outline map of the Ocean Springs, Mississippi, area. The dot shows where the fiddler crabs were collected.

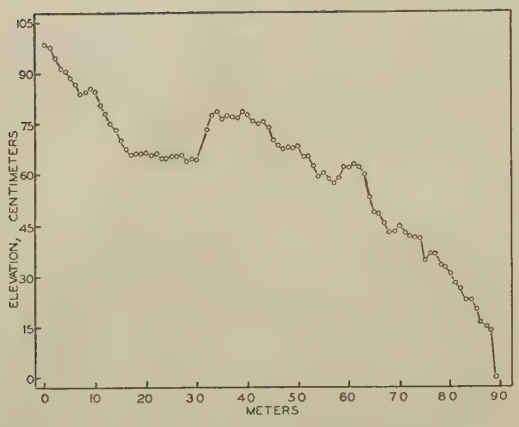


FIG. 2. Contour of the portion of the beach where the fiddler crabs were collected.

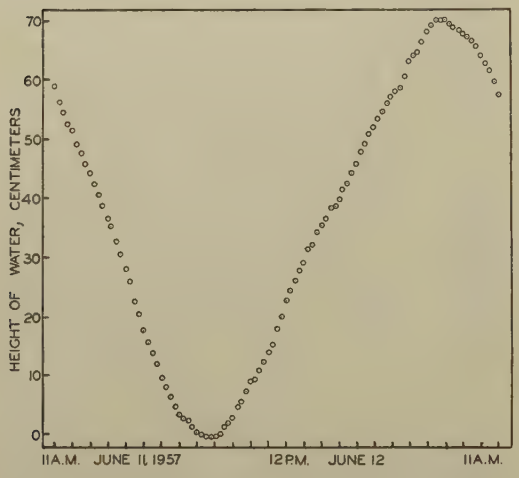


FIG. 3. Height of water above the low tide level from 11 A.M. on June 11, 1957, until noon of June 12 on the portion of the beach where the fiddler crabs were collected.

only 0.985 meter. As evident from inspection of Figure 2 the beach at Ocean Springs is typical of most beaches: elevation decreases rapidly near the high and low tide marks. This beach has a slight elevation in the middle of the intertidal zone.

From 11 A.M. of June 11, 1957, through noon of June 12 the distance from the top of a stake firmly fixed in the water below the low tide mark to the surface of the water was measured at 15-minute intervals to determine the times of high and low tides as a verification of the diurnal nature of the tides on the beach. After the measurements were completed the data were converted to height of water above the low tide level and plotted versus time of day (Fig. 3).

The times when the areas where the burrows were located began to uncover and when the crabs from each area first appeared on the surface were also noted. On June 12 the moon was full and at its maximal southern declination. Therefore, tropic tides prevailed. As is typical of tides, the height of the water changed slowly near times of high and low tides and rapidly in between (Fig. 3). Low tide occurred at 7:45 P.M. on June 11, high tide at 8:45 A.M. on June 12. Twenty-four hours and 49.3 minutes or 24.8 hours, the typical diurnal tidal frequency, were required for the water to return to the height it was when measurements were started. The water rose 69.9 centimeters.

To determine the rate the water receded

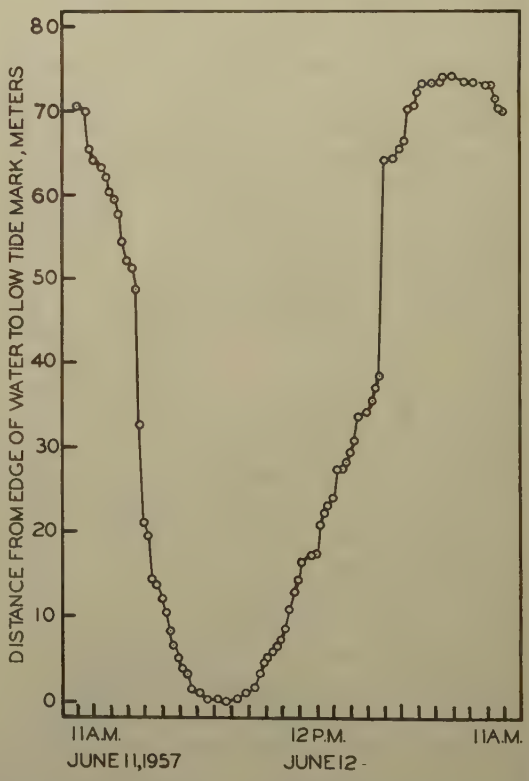


FIG. 4. Distance from edge of water line to low tide mark from 11 A.M. on June 11, 1957, through noon of June 12 on portion of beach where the fiddler crabs were collected.

from the high tide to the low tide mark and then advanced, the distance from the stake below the low tide mark to the water's edge was measured whenever the height of the water was determined. The data are presented in Figure 4 where the distance from the water's edge to the low tide mark is plotted versus time of day. As would be anticipated from the contour of the beach and rate of rise and fall of the tide (Figs. 2 and 3), the water advanced and receded slowly near the high and low tide marks whereas rapid movements occurred near the middle of the intertidal zone.

*Semilunar rhythm of color change in fiddler crabs obtained from burrows above the high tide mark*

*Uca pugilator* were found living in burrows above the high tide mark. These burrows would be covered only in the event a severe storm caused exceptionally high tides. On June 11 and 12 about 300 of these crabs were collected and returned to New Orleans. Beginning on June 13 the average chromatophore stage of 50 crabs selected at random from the aquarium was determined hourly from 8 A.M. through 7 P.M. every second day through July 5. On June 22 a second batch of several hundred of these crabs was collected and returned to New Orleans. The latter group was observed in like manner every second day from June 23 through July 5. Since the two batches were rhythmically similar, the data for both groups were averaged so that each observation from June 23 onward represents the average of 100 crabs.

The data obtained from June 13 through July 5 are presented in Figure 5 to illustrate the nature of the results obtained. A 24-hour rhythm of color change was exhibited by the crabs; every 24 hours the crabs would darken by day and then blanch at night.

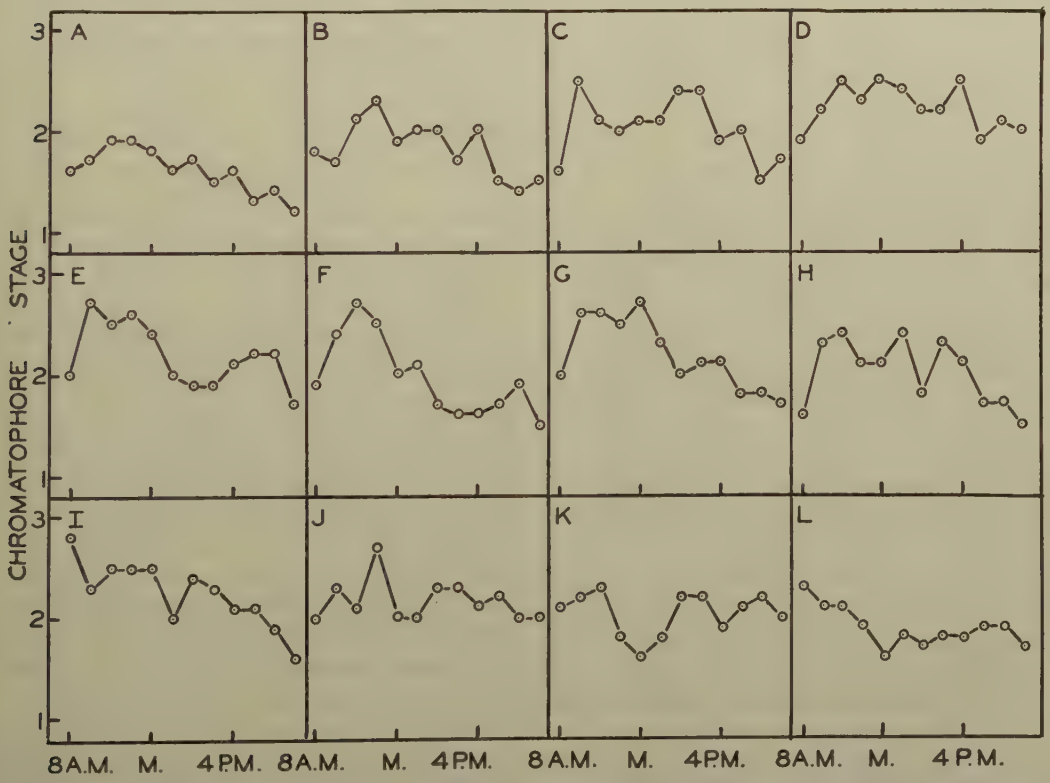


FIG. 5. Mean changes in the degree of melanin dispersion of 50–100 specimens of *Uca pugilator* obtained from burrows above the high tide mark. The crabs were observed every second day from (*A*) June 13, 1957, through (*L*) July 5.

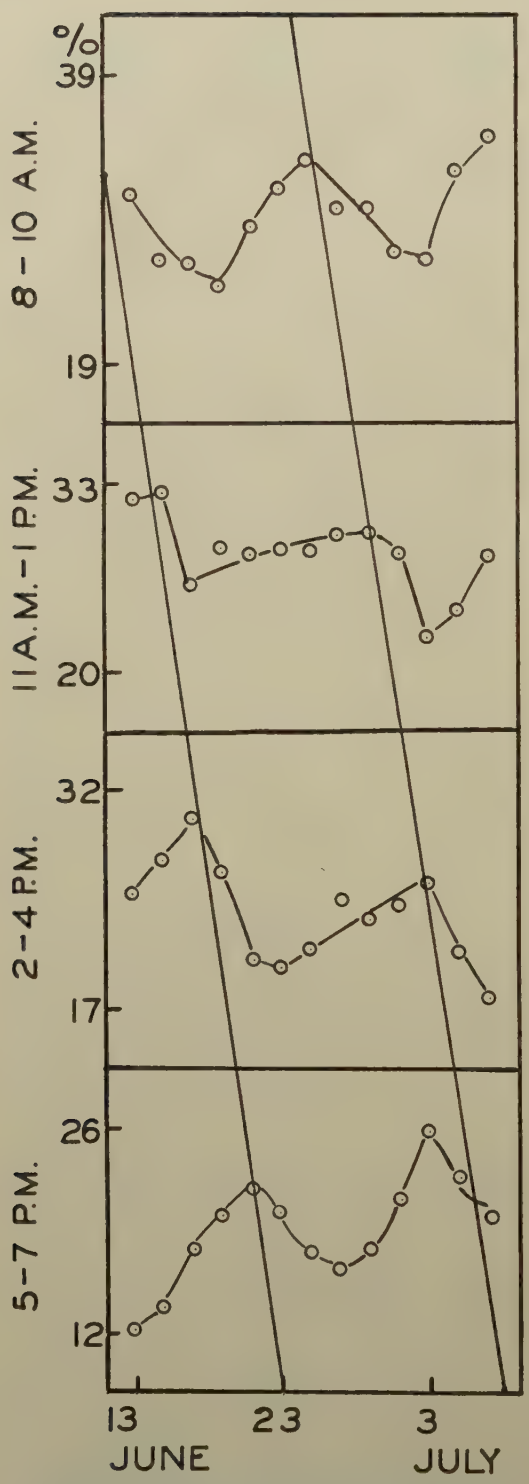


FIG. 6. Relation between percentage of daily melanin dispersion of *Uca pugilator* occurring at each of four periods during the day and the day of the month. These crabs were collected from burrows above the high tide mark. Note the tidal maxima passing over the daily periods at the tidal rate of approximately 48.8 minutes per day. A 14.8-day cycle, the interval between the parallel diagonal lines, was apparent.

This rhythm and the rhythms described below were persistent and endogenous. Since the crabs were kept in darkness and not exposed to environmental influences of alternating light and dark periods and high and low tides, the rhythms correlated with but were not controlled by the environmental events.

The daily patterns, however, did not show the typical tidal rhythm found in fiddler crabs living in the intertidal zone (Brown *et al.* 1953, Fingerman 1956). The time of maximal pigment dispersion did not progress across the day and then return to 8 A.M. Rather, the maximum of each curve was restricted to the hours between 8 A.M. and noon with no evidence of progression, decidedly different from the results obtained by Fingerman (1956) for the same species collected at Ocean Springs but living in the intertidal zone.

However, as is evident from closer inspection of Figure 5, the daily curves were not the same each day. The melanin on some days would gradually become more concentrated throughout the day (*e.g.*, I and L in Fig. 5) and on other days would remain fairly well dispersed (*e.g.*, D and J in Fig. 5).

To determine if tidal and semilunar rhythms of color change were present but were being suppressed by the 24-hour rhythm, the data were subjected to the following type of analysis. The 12 times of observation during the day were grouped into 4 periods of three hours each, 8–10 A.M., 11 A.M.–1 P.M., 2–4 P.M., and 5–7 P.M. The percentage of the total daily excursion of the pigment that each three-hour period occupied was then calculated. To obtain a base for calculating the percentages, the 12 hourly averages were summed and 12 subtracted from the total, because if there had been no daily excursion of pigment the sum would have been 12. Similarly, the average chromatophore indices for each three-hour

period were summed and three subtracted from the total. The percentage of the total that each three-hour period occupied was then calculated. The data are presented in Figure 6. The maxima and minima progressed at a rate closely approximating the rate at which a tidal rhythm would be expected to progress. The parallel diagonal lines were drawn through the maxima of the curves of the calculated percentages for each three-hour period at a distance of 14.8 days apart, the expected average interval between days on which a low and a high tide will occur at the same time of day where the tides are diurnal. Therefore, endogenous, persistent tidal and semilunar rhythms of color change were present in these fiddler crabs that were out of contact with their original habitat during the period of observation. The overt expression of the tidal cycle, however, was suppressed by the 24-hour rhythm of color change. Comparison of the times of high and low tide at Ocean Springs with the times of the maxima in Figure 6 indicated that the maxima tended to coincide with the times of high tide. This coincidence with the times of high tide did not occur each day because of the irregularity of diurnal tides when the moon is in the plane of the equator.

*Phase difference in the tidal and semilunar rhythms of color change*

This series of observations was undertaken to analyze further the phase difference between the tidal rhythms of color change of fiddler crabs collected from two different portions of the beach to determine if the predicted 9.1-hour phase difference mentioned above would occur.

The times that the burrowing areas of both sets of crabs were uncovered by the receding tide were determined. The first appearance of fresh holes made by crabs in the burrows was also observed, since the openings into the burrows are normally sealed when the tide is high. The region of the low tide burrows began to uncover at 5 P.M. on June 11; holes from the burrows to the surface first appeared at 9 P.M. The portion of the beach where the high tide burrows were located began to uncover at 10:30 A.M. on June 12, 1.75 hours after high tide; openings into the burrows first appeared 75 minutes later. The disparity in times required for the first appearance of crabs from the two areas, 4 hours versus 1.25 hours, was probably due to the nature of the substratum. The burrows of the group near the high tide mark were in coarse sand that drained more rapidly than the mud in which the crabs close to the low tide mark lived. Therefore, the former crabs would be able to come to the surface sooner.

The phase difference in the tidal rhythms of the groups expected in the laboratory, based upon the difference in times of uncovering the portion of the beach where the crabs lived, was 7.3 hours. This difference was calculated as follows. High tide at Ocean Springs occurred 48.8 minutes earlier on June 11 than on June 12, *i.e.* at 7:56 A.M., and the burrows near the high tide mark must have begun to uncover at 9:41 A.M. From 9:41 A.M. to 5 P.M. is 7 hours and 19 minutes or 7.3 hours.

The phase difference based upon the differences in the times of first appearance of holes leading from the burrows was 10.1 hours. This figure was calculated as follows. Holes of the low tide group first appeared 4 hours after the burrowing area began to clear; openings into the burrows first appeared in the area of the high tide group 75 minutes after the water began to uncover their area. The difference between 4 hours and 1.25 hours is 2.75 hours. This value added to 7.3 hours yields a total difference, rounded off to the nearest tenth, of 10.1 hours.

On June 11 and 12 several hundred crabs from the high tide burrows and 32 crabs from the low tide burrows were collected and returned to the laboratory. Fifty of the former and all of the latter crabs were observed hourly every second day from 8 A.M. through 7 P.M. beginning June 13 until July 7. Twenty of the low tide group survived the entire period of observation. On June 22 a second group of crabs from each area was collected. In the second collection several hundred crabs had been obtained from the high tide burrows but only 37 low tide crabs were obtained. The

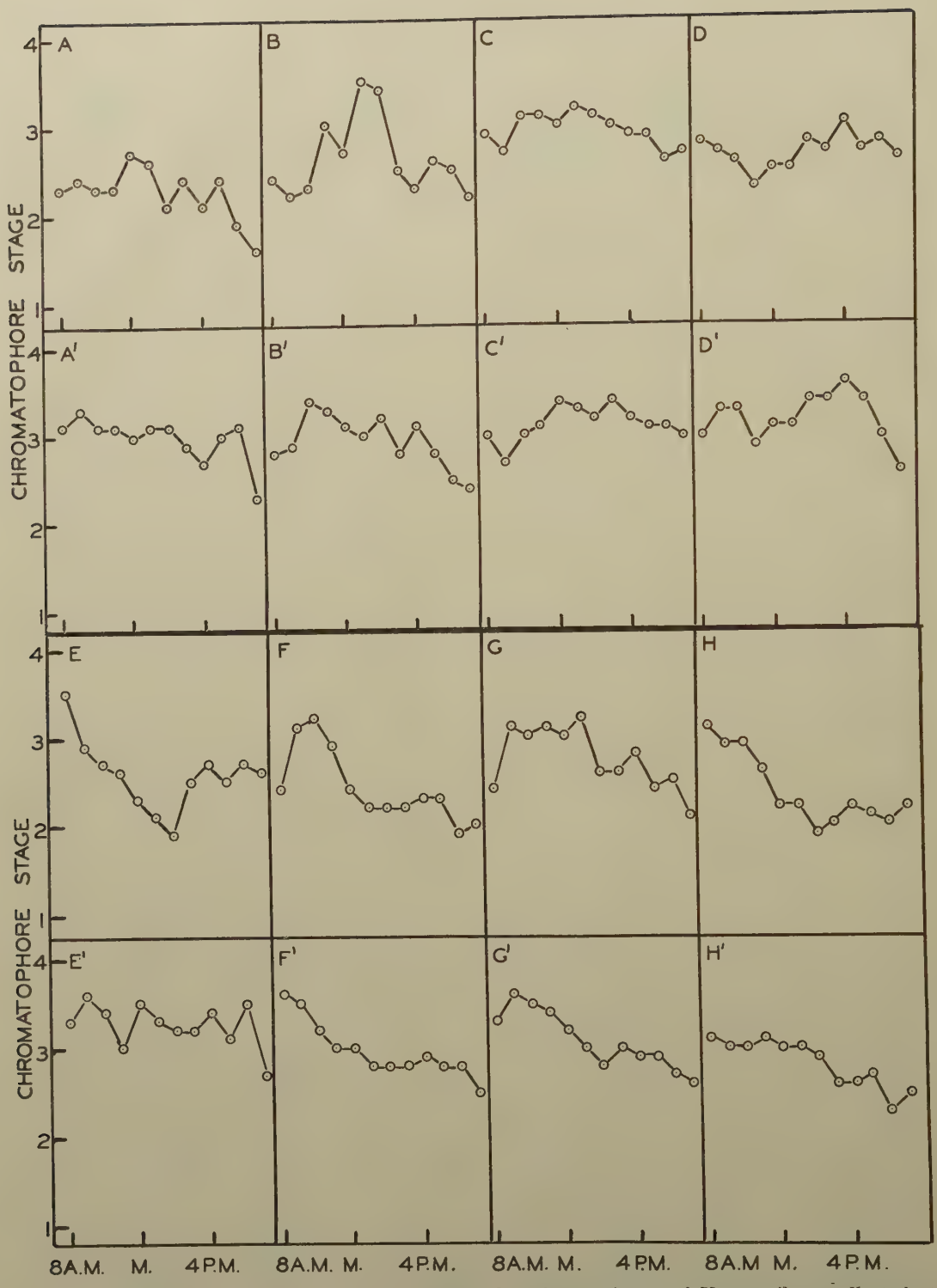


FIG. 7. The mean patterns obtained on several days for specimens of *Uca pugilator* collected at Ocean Springs. Sections *A* through *H* represent crabs collected near the high tide mark; sections *A'* through *H'* crabs collected near the low tide mark. *A* and *A'*, June 13; *B* and *B'*, June 15; *C* and *C'*, June 17; *D* and *D'*, June 19; *E* and *E'*, June 21; *F* and *F'*, June 23; *G*, June 29; *G'*, June 25; *H*, July 5; *H'*, July 7.

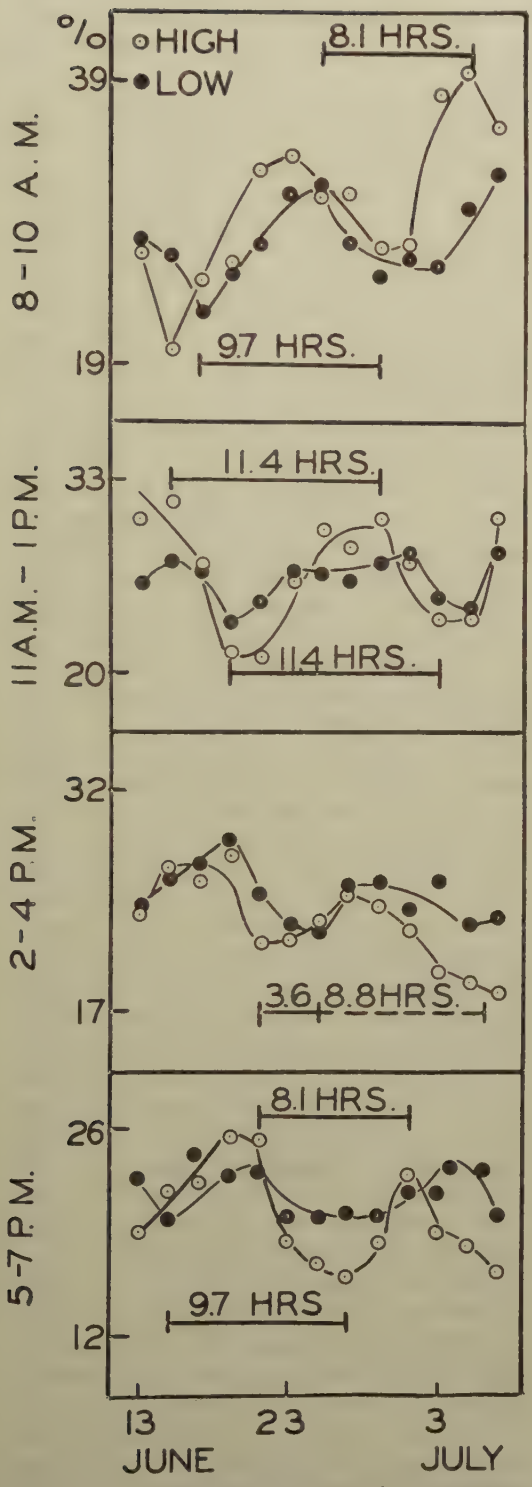


FIG. 8. Relationship between the percentage of daily melanin dispersion of *Uca pugilator* occurring at each of four periods during the day and the day of the month. Circles represent crabs collected near the high tide mark; dots, near the low tide mark. The phase differences between the groups were converted to hours on the basis of the fact that a tidal cycle progresses across the 24-hour day at the average rate of 48.8 minutes per day. See text for complete explanation.

number of the latter gradually dwindled to 26 by the last day of observation. The crabs from the second collection were treated in the same manner as those of the first collection. Both groups were rhythmically similar to the corresponding groups of the first collection. The data of the corresponding groups from June 23 on were averaged. Part of the data is presented in Figure 7. All of the data were used to produce Figure 8, which was prepared in the same manner as Figure 6.

Inspection of Figures 7 and 8 reveals that both groups of crabs displayed a tidal rhythm of color change similar to that described previously for the same species collected in the same area (Fingerman 1956, 1957b). In both the high and low tide groups the maximum of pigment dispersion shifted across the day, as would be expected in an overt tidal rhythm. In the high tide group maximum pigment dispersion occurred at 8 A.M. on June 21 and again July 5 whereas in the low tide group this happened June 23 and July 7, *i.e.*, 14 days were required for the peak to move across the curve and return to the beginning, closely approximating the average tidal frequency of 14.8 days. This situation was entirely different from that depicted in Figure 5 where maxima occurred between 8 A.M. and noon only, whereas in Figure 7 maxima are shown both in the morning and the afternoon. Not only did the peaks in Figure 7 move but the general character of the curves changed as the maximum moved into the afternoon; the average chromatophore indices determined in the afternoon showed a general increase relative to the morning ones. The maxima and minima shown in Figure 8 also moved across the day until they occurred in the 5–7 P.M. portion of the day. Then they would again occur at 8–10 A.M. and once again start to move across the day.

Inspection of Figures 7 and 8 likewise

reveals that the tidal rhythms of the two groups were out of phase with one another. On any given day with the possible exception of June 17, *e.g.*, June 13 and 15, the maximum of the high tide group was displaced approximately three hours to the right of the maximum of the low tide crabs. This relationship remained fixed during the entire period of observation in the laboratory. Further evidence of a phase difference was the fact that the shift of the maximum back to the early morning hours did not occur on the same day for both groups of crabs but rather two days apart on two occasions, June 21 and 23, and then again July 5 and 7. The rhythms of these crabs could not have been in phase with one another and still shift two days apart on two separate occasions 14 days apart.

In the environment as the water receded from the high tide mark to the low tide mark the region of the burrows of the high tide group had to be uncovered prior to the area of the low tide group. The times of supplemental pigment dispersion due to the tidal rhythm are set in accordance with the times of high and low tides (Brown *et al.* 1953). Therefore, the tidal maximum of the high tide group could not have occurred about three hours later each day than that of the low tide group but rather about 9.5 hours earlier, since in a tidal cycle displacement of a curve about three hours to the right is equivalent to displacement about 9.5 hours to the left.

As a result of the phase difference between the two groups of crabs the shift of the tidal maximum back to the left end of the curve apparently occurred about two days earlier for the high tide group than for the low tide group (E and F′ in Fig. 7). Since data were obtained every other day only, closer approximation of the date of the shift was not readily possible. However, according to the same reasoning employed in the paragraph above, the shift of the high tide group relative to the low tide group could not have occurred two days earlier but actually would occur about 12.5 days later (Fig. 7H). In portions F, G, and G′ of Figure 7 gradual shifting of the tidal maximum across the day was shown again. Before observations were completed the maximum in the curve of each group again shifted to the left end of the curve.

Since examination of the beach revealed (1) that on any given day the area of the high tide group began to uncover 7.3 hours earlier each day than the area of the low tide group, and (2) that the latter crabs appeared on the surface 10.1 hours later than the former crabs, the area of the high tide crabs would begin to uncover at any given hour of the day (*e.g.* 10 A.M.) about 9.0 days later than the area of the low tide group. This is the number of days required for the tidal cycles to progress about 7.3 hours. Similarly, crabs of the high tide group would appear on the surface at any given hour of the day, on the average, about 12.4 days later than the crabs living in the low tide area.

Inspection of the dates on which maxima and minima occurred in each period of the day (Fig. 8) for crabs collected from the two areas revealed a general displacement of the high tide curves about 11.9 days to the right of the curves of crabs from the low tide area. The differences between the times of maximal and minimal tidal effects for the two groups of animals, respectively, have been converted into hours on the basis of tidal cycles progressing over the 24-hour cycle at an average rate of 48.8 minutes per day. The average phase difference was 9.8 hours. Therefore, the phases of the tidal rhythms of crabs living closer to the high tide mark are set 9.8 hours earlier than the phases of the rhythm of low tide crabs. This value lies between the values observed in the field—7.3 hours for the time required for the receding water to go from the high tide area to the low tide area, and 10.1 hours as the interval between the first appearance of crabs in the two areas.

The final series of observations was performed from June 13 through 25 on a group of *Uca minax* collected in the high tide area. The data for the two days of observations that indicate the phase relations are shown in Figure 9. Thirty-two crabs were alive on June 19, and 27 on June 21. On June 19 the maximum occurred at 7 P.M., then the curve changed shape as the tidal effect

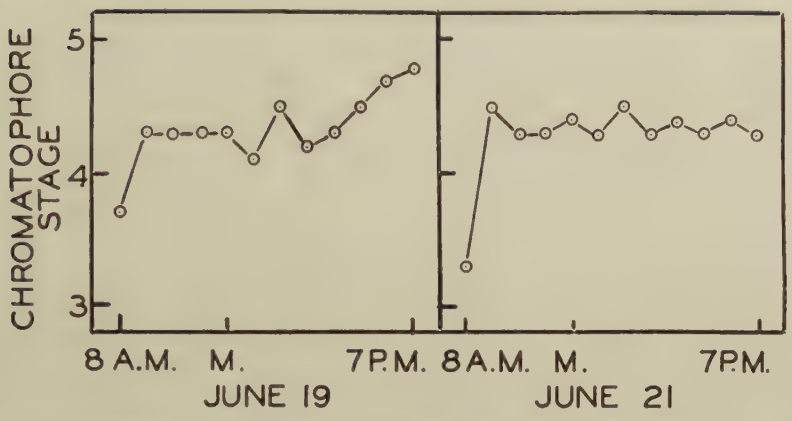


FIG. 9. Mean changes in the degree of melanin dispersion in specimens of *Uca minax*.

shifted to the early hours of the day. A shift of maximal effect from one end of the day occurred on the same date for the high tide specimens of *Uca pugilator* (Fig. 7). Specimens of the two species taken from the same portion of the beach were in phase with one another. The characters of the curves were different however. The melanin of *Uca minax* remained nearly maximally dispersed throughout the period of observation in contrast to the melanin of *Uca pugilator* which exhibited from 8 A.M. through 7 P.M. a wide range of variation in degree of dispersion.

## DISCUSSION

The character of the daily patterns of color change of fiddler crabs collected from burrows above the high tide mark (Fig. 5) was different from that reported by previous investigators of tidal rhythms of color change in crabs from the intertidal zone (Brown *et al.* 1953; Fingerman 1956, 1957b). The tidal maximum of pigment dispersion of the crabs that lived above the high tide mark did not gradually shift across the day. As a result, no overt tidal rhythm of color change was evident. However, analysis of the data by percentages (Fig. 6) revealed typical tidal and semilunar rhythms of color change. Overt expression of the tidal cycle was apparently suppressed by the 24-hour rhythm, since the crabs living in the burrows not normally covered at high tide could leave their burrows at any time during the day rather than be forced to wait until the burrowing area was uncovered by the receding water as fiddler crabs living in the intertidal zone must do. The tidal rhythm is apparently as deep-seated as the 24-hour rhythm. The latter, however, is endowed with the ability to suppress the overt expression of the former.

In contrast to the character of the rhythm of the fiddler crabs living above the high tide mark, the tidal cycles of both groups of fiddler crabs living in the intertidal zone (Fig. 7) were the same as those described previously by the authors cited above. The gradual progression across the day of the maximum that occurred on the average 48.8 minutes later each day resulted in the appearance of a semilunar rhythm, because the tidal and 24-hour rhythms only repeated similar time relations to one another on the average once every 14.8 days.

As mentioned above, the sum of the phase differences observed during the summers of 1955 and 1956 was 9.1 hours. The phase difference observed herein (Fig. 8) was 9.8 hours. These results indicate that phase differences are additive and give further support to the concept that the times of supplemental pigment dispersion due to the tidal rhythm are set according to the tidal events occurring within a localized area of the beach (Fingerman 1956, 1957b). Since the rhythms are persistent and endogenous at least in part, the phase difference between the high and low tide groups remained when the crabs were removed from their habitat for observation in the laboratory.

The time of supplemental pigment dispersion due to the tidal rhythm was set perhaps primarily according to the time the area was uncovered by the receding water and secondarily according to the time required for the area to drain so that the sand was firm enough to support openings to the surface from the burrows. This concept helps explain the fact that crabs living near the high tide mark first appeared 75 minutes after the area started to uncover, whereas crabs living near the low tide area did not appear until 4 hours after their region started to uncover. This difference in times of first appearance could not have been due to differences in size of locale because the high tide area was approximately 5.4 times as large as the low tide area, whereas 3.2 times as long was required for the low tide crabs to appear as for the high tide crabs.

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# Substrates as a Factor in Shrimp Distribution[1]

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ABSTRACT

Three species of Western Atlantic penaeid shrimps—*Penaeus setiferus*, *P. aztecus*, and *P. duorarum*—were allowed a free choice among five types of substrates in partitioned experimental troughs. The substrates used were beach sand, shell-sand, muddy sand, sandy mud, and loose peat. Each species was tested separately, and each experiment was replicated once. Results of the experiments showed that distribution of the shrimps on the different substrates was not random. In each experiment departures from the expected distribution were statistically significant. *P. duorarum* occurred most often on shell-sand. *P. aztecus* and *P. setiferus* were found most frequently on the softer, muddier substrates—loose peat, sandy mud, and muddy sand.

Food content in the bottom materials may have been a confounding factor, but the results indicate attraction to substrate aside from the possible attraction to food.

Water volume, or pore space, and the compaction of bottom materials, may influence the degree of burrowing.

The geographic and bathymetric distribution of *Penaeus setiferus* (Linn.), *P. aztecus* Ives, and *P. duorarum* Burkenroad in the Western Atlantic is rather well known (Burkenroad 1939, Broad 1950, Springer and Bullis 1954, Hildebrand 1954, 1955, and others). Local patterns of distribution are known in detail for certain well-studied areas, but the influence of environmental factors on these patterns is still not understood. The role of salinity has been discussed as a limiting factor in estuarine nursery areas (Burkenroad 1939, Gunter 1950, Hildebrand and Gunter 1953, Gunter and Hildebrand 1954, Williams 1955a, b), but the role of such factors as cover, temperature, food, turbidity, and substrate has been treated with less thoroughness. Williams (1955a) discussed the influence of cover on estuarine distribution, and others have considered the subject briefly. Temperature has been treated chiefly in relation to winter kill or low temperature tolerance (Gunter and Hildebrand 1951, Williams 1955a, Lindner and Anderson 1956). Food habits have been considered in general terms which are reviewed in the discussion below. Effects of turbidity have received casual mention by a number of writers, and records concerning relationships between the species and substrates have chiefly dealt with abundance of shrimp and trawlability of bottoms.

Among animals so closely associated with the bottom as are littoral penaeids it appears that nature of the substrate may have an important influence on distribution. Many observations attest to this, for it is common knowledge among shrimp fishermen and others that these species are often found on certain types of bottom. However, at other times these mobile animals may search widely for food or cover and be in a measure independent of bottom type, especially during the migration from estuaries to the sea. Factual knowledge of these relationships is not well established. It is not known whether distribution may largely be governed by the nature of the substrate independent of the food supply, or whether favored habitats are those which harbor food regardless of substrate composition. The possibility of species attraction to bottom type has not been investigated.

In North Carolina estuaries shrimp distribution is not uniform. Density of

[1] I wish to thank Dr. Bernard Pasternack, Dept. of Biostatistics, University of North Carolina for counsel in planning the statistical approach to this problem, and my colleagues for counsel and criticism of the manuscript.

specific aggregations varies with relative distance from the sea, salinity, and perhaps bottom type (Williams 1955b). Other areas show similar distribution patterns (Burkenroad 1939, Gunter 1950). Williams (1955a, b) also has shown that young *P. duorarum* and *P. aztecus* utilize many of the same nursery areas but at different times of year, while *P. setiferus* of similar age use nursery grounds in somewhat fresher water. Springer and Bullis (1954) and Hildebrand (1954, 1955) have discussed littoral penaeid distribution relative to bottom types in the Gulf of Mexico, pointing out that *P. setiferus* and *P. aztecus* are found in greater densities over bottoms of terrigenous silt, whereas *P. duorarum* is found in greater densities over calcareous mud and sands or mixtures of shell and sand. Such distribution patterns suggest that these forms may have definite requirements in bottom type and that attraction to substrate could be determined by experimentation.

In view of the cited evidence, and other published observations, a laboratory experiment with substrates was designed to test the following null hypothesis: subadult *P. setiferus*, *P duorarum*, and *P. aztecus* are not attracted to particular bottom types. If this hypothesis was confirmed, substrates would be considered to have little or no influence on shrimp distribution. If the hypothesis was rejected, some influence, possibly substrates, could be causing departures from the expected distribution.

## MATERIALS AND METHODS

Five bottom types which are widely but not uniformly distributed over North Carolina estuaries were chosen for use in the experiment. Four substrates taken from a shallow tidal stream, Broad Creek, approximately 12 miles west of Morehead City, Carteret County, consisted of loose peat, sandy mud, muddy sand, and a shell-sand mixture. The first three substrates were obtained with a shovel from the upper four inches of subtidal bottom, and the shell-sand was taken from the low water line. Samples were brought to the laboratory in enamel buckets. The fifth material was clean sand from a beach on Bogue Sound. These selections were representative of bottoms in local estuaries.

Table 1. *Approximate particle-size distribution expressed as per cent by weight, and a soils classification for four kinds of substrate*

| | Shell-sand | Sand | Muddy sand | Sandy mud |
|---|---|---|---|---|
| >2 mm shells, stones & debris | 30.10 | | | |
| 2->1 mm very coarse sand | 1.32 | 2.00 | 0.43 | 1.03 |
| 1->.5 mm coarse sand | 15.50 | 14.12 | 2.83 | |
| .5->.25 mm sand | 33.35 | 62.30 | 17.13 | 5.30 |
| .25->.1 mm fine sand | 11.15 | 13.32 | 55.33 | 58.60 |
| .1->.05 mm very fine sand | 1.90 | 3.72 | 10.03 | 10.00 |
| 50 $\mu$->20 $\mu$ coarse silt | 2.50 | 2.50 | | 2.50 |
| 20 $\mu$->2 $\mu$ silt | 2.50 | 2.50 | 7.50 | 17.50 |
| 2 $\mu$-<2 $\mu$ clay | | | | 2.50 |
| air-dry moisture content | 0.27 | | 0.13 | 0.65 |
| | 98.59 | 100.46 | 93.38 | 98.08 |

Four of the bottom types were subjected to standard methods of mechanical analysis, particles larger than .05 mm being graded with sieves, and smaller sizes by the Bouyoucos hydrometer method (Sanders 1956; and C. H. M. van Bavel, U.S.D.A., North Carolina State College, personal communication). The results of these analyses (Table 1) are approximations, for they are from single samples. No estimate of the range of variation was made, though observation indicates that the >2 mm fraction of the shell-sand is subject to great variation. The muddy sand and sandy mud both fit the designation "loamy fine sand" (Soil Survey Staff 1951). The fifth substrate, loose peat, is essentially a mat of organic debris, and though it contains some silt and sand, particle-size distribution does not fairly describe its structure. Because of the high content of vegetable debris, a large quantity of water is contained in this substrate. Three 1000-ml samples had a mean weight of 1121 g. The mean air-dry volume of these samples (lightly packed) was 306 ml, the mean air-dry weight was 249 g and the mean oven-dry weight, 232 g. Air-dry shrinkage in volume was 77 per cent; oven-dry shrinkage in weight was 79 per cent.

The experiment was designed to allow animals a free choice among these five substrates under uniform conditions in the

absence of food. To do this two redwood troughs were constructed: one 8 feet x 2 feet x 10½ inches, and the other 8 feet x 1½ feet x 10½ inches. Each was divided into five cells approximately 1½ feet long with a six-inch cell at one end serving as a drain. The cells were partially separated by boards 7 inches high, drilled with three one-inch holes with a separator at the drain end 8¾ inches high serving as a dam. The dams could be opened for draining the troughs. Depth of the substrates was approximately two inches. The troughs were covered with removable plastic screens to keep the animals from jumping out. No attempt was made to regulate the amount of light entering the troughs. The room was dark at night. At first running sea water was introduced directly into each cell, but excessive turbidity finally left no choice but to filter the water through shell-sand and introduce it in the ends opposite the drains. The water was pumped directly from Bogue Sound through a system of polyethylene tubing.

Shrimp were subjected to weekly periods of observation in the troughs, and fresh animals were used in each trial. A total of 20 shrimp per trough was assumed to be the maximum tolerance without crowding. Four shrimp were introduced into each compartment at the beginning of each weekly trial. Fresh substrates were used at each new trial except in a few instances when some materials were used for two successive trials.

In such a free-choice situation, if no attraction to bottom type was exhibited, shrimp would be expected to have frequented the different cells in approximately equal numbers after many trials. However, compartments arranged in a row tend to preclude such assortment because the first and fifth in each trough differ essentially from the other three in that for these the shrimp can move into only one adjoining cell whereas for the middle three they can move into either of two neighboring cells. Therefore, the first and fifth cells might tend to retain a greater number of animals than the others. This difficulty was avoided by running the experiment in a randomized latin-square design which allowed each bottom type to occur in every position once. The design required five different arrangements of substrates. In practice, three of these occurred in the wide and two in the narrow troughs during the first experiment. In the replication, trough use was reversed. The use of a circular arrangement of cells as reported by Lindroth (1953) could probably be adapted to this type of experiment, thus avoiding use of the latin-square design.

Results from counts of shrimp were subjected to a chi-square test of the null hypothesis. In order to obtain a valid chi-square test, the total number of observations must be fixed in the sampling procedure; however, in this instance such fixation was rendered difficult by turbidity, for the nature of the muddier substrates hindered accuracy in the counts. Usually erroneous counts were under 20. Death of a shrimp or occasional escapement from the troughs also marred the counts, although such occurrences were uncommon. Because the total number of observations was fixed (*i.e.*, each total count had to be 20) adjustments in erroneous counts were necessary in order that the limiting distribution of the test statistic would obey the chi-square distribution. If, for example, there was an under count, say 16, adjustment could be made in the following ways: (1) assign each of the remaining four shrimps at random to the five cells, (2) assign the remaining four shrimps in proportion to the observed distribution of the 16 shrimps in the five compartments, or (3) run an experiment to estimate the distribution of the missed shrimps and allocate the four individuals according to this distribution. Conversely, if there were an over count, deductions could be made in a similar manner. Only (1) and (2) were considered practical. Of these procedures the first conceals differences that may exist and hence favors the null hypothesis of "no attraction," whereas the second favors the alternate hypothesis. A modification of the first procedure was used. The beach-sand and shell-sand cells were always reasonably clear and could be counted

accurately, but the loose-peat, muddy-sand, and sandy-mud compartments were often turbid due to activity of the animals. Adjustments on observations of *P. duorarum* were applied at random to all bottoms except beach sand, but random adjustments were necessary only on the three muddy bottoms with *P. aztecus* and *P. setiferus*.

Dead shrimp were replaced by recently caught animals from a reserve tank. Counts were made with the aid of a T-shaped piece of metal on the end of a stick which was used to dislodge buried shrimp. Counts at first were made in the morning, afternoon, and at night. Soon only the morning count was recorded, and only it has been used in the calculations. *P. duorarum* and *P. aztecus* are quiet during the day and most active at night; hence the only valid count for these species would be one made after a nighttime period of free movement with no disturbances. *P. setiferus*, more active at all times, was counted so far as possible in the same manner. Chi-square values were calculated from adjusted counts (Table 2).

Temperatures were taken by thermometer in the experimental troughs and by a continuous-recording device in Bogue Sound near the pump intake. Inside water temperature was usually within one degree of outside surface water temperature—warmer in winter, cooler in summer. Salinity records were kept weekly after April 1.

TABLE 2. *Results of morning counts of three species of shrimps on five kinds of substrate* All $\chi^2$ values are significant at the 1% level for 4 D.F.

| | Total Count | % Total | Total Count | % Total |
|---|---|---|---|---|
| | *Penaeus duorarum* | | | |
| | Jan. 23–Feb. 18 | | March 15–April 18 | |
| Sand | 111 | 15.9 | 107 | 15.3 |
| Shell-sand | 186 | 26.6 | 175 | 25.0 |
| Loose peat | 127 | 18.1 | 161 | 23.0 |
| Muddy sand | 129 | 18.4 | 120 | 17.1 |
| Sandy mud | 147 | 21.0 | 137 | 19.6 |
| Total | 700 | 100.0 | 700 | 100.0 |
| | $\chi^2 = 23.96$ | | $\chi^2 = 22.60$ | |
| | *Penaeus aztecus* | | | |
| | May 18–June 16 | | June 19–July 10 | |
| Sand | 96 | 13.7 | 76 | 10.8 |
| Shell-sand | 37 | 5.3 | 47 | 6.7 |
| Loose peat | 225 | 32.1 | 209 | 29.9 |
| Muddy sand | 152 | 21.7 | 145 | 20.7 |
| Sandy mud | 190 | 21.1 | 223 | 31.9 |
| Total | 700 | 99.9 | 700 | 100.0 |
| | $\chi^2 = 160.00$ | | $\chi^2 = 174.42$ | |
| | *Penaeus setiferus* | | | |
| | July 19–Aug. 10 | | Aug. 10–30 | |
| Sand | 65 | 9.3 | 104 | 14.7 |
| Shell-sand | 58 | 8.3 | 67 | 9.6 |
| Loose peat | 224 | 32.0 | 252 | 36.0 |
| Muddy sand | 131 | 18.7 | 89 | 12.7 |
| Sandy mud | 222 | 31.7 | 188 | 26.9 |
| Total | 700 | 100.0 | 700 | 99.9 |
| | $\chi^2 = 187.21$ | | $\chi^2 = 171.95$ | |

## RESULTS

### *Penaeus duorarum*

Experimentation was begun with *P. duorarum* in January 1957. An example of representative counts and adjustments is given in Table 3. Results of adjusted total counts in the first run and its replication are shown in Table 2. Outside temperatures during the two periods were not comparable, those during the first run ranging from 6 to 16°C, those in the second from 13 to 19°C. Salinities during the whole period had an approximate range of 25 to 32‰. The mean total length of animals used in the first experiments was approximately 50 mm, that of animals in the second experiments approximately 60 mm.

This species, notably, can burrow into an extremely coarse substrate. Both replications show that shell-sand is an attractive substrate, though in the warmer period loose peat bottom was frequented nearly as often. Most of the animals remain burrowed during the day with only the ommatidial surfaces and a portion of the rostrum visible. In shell-sand the animals were often completely buried, as deep as the trough planking, and the only way they could be counted was by digging because they were reluctant to move. At night the

TABLE 3. *Actual counts (with adjustments) made of* Penaeus duorarum *during the week of March 15, 1957*
O = observed. A = adjusted.

| Days | 15 | | 16 | | 17 | | 18 | | 19 | | 20 | | 21 | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | O | A | O | A | O | A | O | A | O | A | O | A | O | A | |
| **Wide-trough cells** | | | | | | | | | | | | | | | |
| Sand | 1 | | 4 | | 5 | | 2 | | 2 | | 2 | | 1 | | 17 |
| Shell-sand | 3 | 5 | 4 | | 4 | | 5 | 6 | 3 | 4 | 9 | | 6 | 7 | 39 |
| Loose peat | 6 | | 6 | | 3 | | 3 | | 3 | 6 | 3 | | 3 | 5 | 32 |
| Muddy sand | 2 | 3 | 4 | | 1 | | 6 | 8 | 3 | | 0 | 2 | 4 | | 25 |
| Sandy mud | 5 | | 2 | | 7 | | 1 | | 4 | 5 | 4 | | 1 | 3 | 27 |
| Total | 17 | 20 | 20 | | 20 | | 17 | 20 | 15 | 20 | 18 | 20 | 15 | 20 | 140 |
| **Narrow-trough cells** | | | | | | | | | | | | | | | |
| Sand | 4 | | 5 | | 7 | | 4 | | 7 | | 5 | | 4 | | 36 |
| Shell-sand | 3 | 4 | 2 | | 2 | | 2 | | 3 | | 2 | 4 | 6 | 7 | 24 |
| Loose peat | 7 | | 5 | | 3 | 4 | 6 | 7 | 4 | | 5 | | 5 | | 37 |
| Muddy sand | 1 | | 5 | | 3 | 4 | 4 | 5 | 5 | | 2 | | 2 | | 24 |
| Sandy mud | 4 | | 0 | 3 | 2 | 3 | 1 | 2 | 1 | | 4 | | 1 | 2 | 19 |
| Total | 19 | 20 | 17 | 20 | 17 | 20 | 17 | 20 | 20 | | 18 | 20 | 18 | 20 | 140 |

shrimp moved freely over and through the separators. In daylight even in the coldest observed inside water temperatures of the winter (8.2°C, Jan. 18), they were active in daylight when disturbed by digging.

*Penaeus aztecus*

Experiments on *P. aztecus* were run from May 18 to July 10 beginning as soon as recruits of the season were large enough to be counted easily (Williams 1955a). Temperatures for the two replications again were not comparable, those during the first experiment ranging from 22 to 29°C, those in the second from 26 to 30°C. Salinities were relatively constant for the two periods, ranging from 31.7 to 35.5‰. The mean total length of animals used in the first experiment was approximately 60 mm and that of those in the second run approximately 85 mm.

In contrast to *P. duorarum* this species occurred most often on the muddier substrates (Table 2), loose peat, and sandy mud, with a slightly lower frequency on the muddy sand. In both replications the results were comparable, although in the warmer period loose peat was relatively less frequented and sandy mud more than in the first run. Turbidity was always greater in water over loose peat and sandy mud, the compartments in which most of the burrowing activity occurred. Changes also occurred on the coarser substrates, occurrence on sand being diminished in the warmer period.

In early arrangements of the first replication the smallest individuals were often found on shell-sand, whereas the large individuals were usually found on softer bottoms. The small shrimp were rarely burrowed in the shell-sand but tended to hide in interstices at the surface of the material, a behavior highly in contrast to *P. duorarum* which actively burrowed into the coarse bottom. In other situations *P. aztecus* like *P. duorarum* burrowed into the bottom until only parts of the eyes and rostra were visible above the surface.

Like its close relative *P. duorarum*, *P. aztecus* exhibited alternating periods of activity and quiescence in the tanks. During daylight most individuals tended to burrow into the muddy bottom, although a few could always be found on the surface. All were active at night.

A common diurnal color change was easily seen in the experimental shrimp. Gray or grayish-brown during the day, *P. aztecus* changed to a reddish brown at night. A few minutes of exposure to artificial light at night elicited suppression of the red-

brown coloration and a return to the paler daytime appearance.

*Penaeus setiferus*

Experiments on *P. setiferus* were run from July 19 to August 30. Temperatures for this period ranged from 22 to 30°C, and, though readings below 25°C were taken in the last week of the second replication, the whole period was nearly uniform. Salinities also were quite steady, ranging from 35.6 to 36.1‰.

This species was the most difficult of the three to collect and bring alive to the laboratory because its body is less firm than that of its congeners, and more easily injured in the collecting trawl. Moreover, it seemed less able to survive transport from the field in barrels. For these reasons, healthy, well-fed specimens were used more than once during the trials. They were maintained in running sea water in outside concrete tanks. Because of the danger of injury to specimens, no attempt was made to measure live animals until the experiments were terminated. The last experimental animals averaged 83 mm in total length, and preceding trials were made with similar or slightly smaller animals.

The muddier substrates (Table 2) were clearly most frequented by *P. setiferus*, loose peat and sandy mud being equally used in the first replication. In the second replication somewhat different occurrences were observed: sandy mud and muddy sand were frequented less, but beach-sand was used twice as much as in the first run. This species is much more active at all times than the other two. This behavior led to difficulties in making counts because movement of the animals kept water over the muddier substrates partially clouded. Therefore, counts had to be made at a time of day (usually morning) when activity and cloudiness were minimal. *P. setiferus* burrows but not with the regularity nor to the extent exhibited by *P. duorarum* and *P. aztecus*. *P. setiferus* presents a different burrowing aspect than the latter two, for the long antennae are conspicuously laid above the surface of the substrate, whereas the shorter antennae of the others are often buried.

DISCUSSION

Results of the experiments agree with the findings of Springer and Bullis (1954) and Hildebrand (1954, 1955) that *P. setiferus* and *P. aztecus* are found predominantly on terrigenous silt bottoms and *P. duorarum* on coral mud or on coarser ground containing mixtures of mollusk shell. In each replication statistical analysis showed that something other than random distribution was at work. These findings also agree with the distribution of juveniles and subadults in North Carolina estuaries where *P. duorarum* is confined largely to areas near the sea where the bottom is composed of coarser materials.

Though results of the chi-square tests are significant in each series of experiments, there may be certain discrepancies in the data (Table 2) which should be pointed out. There is a departure from close agreement between the replications in three instances. *Penaeus aztecus* occurred on sandy mud 21 per cent of the time in the first and 31.9 per cent in the second series of tests. This difference of 10.8 per cent in occurrence between experiments is the largest in the series. *Penaeus setiferus* occurred on sand 9.3 per cent of the time in the first, 14.7 per cent in the second series, and on muddy sand 18.7 per cent in the first, and 12.7 per cent in the second replication. These differences in occurrence are 5.4 and 6.0 per cent respectively. The reason for such discrepancies is not known, but under the experimental conditions in which the only factor under control was the bottom type, such variations between experiments might be expected.

Results indicate that differences in the attractiveness of substrates exist, but the experiment was not designed to answer the question of why such differences are exhibited. Here conjecture must suffice until the facts are forthcoming. Food undoubtedly plays a major role in distribution. Of the confounding factors that might have biased these experiments, food is perhaps paramount. The dry beach sand was nearly devoid of organic matter as was the shell-sand, but the muddy substrates contained much more organic matter, some

undoubtedly living. Part of this material may have been utilized as food by the captive animals.

Food habits of the littoral penaeids are not well established although a number of observations and minor studies have been recorded. Stomach content analyses (Williams 1955a) have shown a variety of ingested materials. Examination of shrimp taken from the experimental troughs showed detritus, plant fragments, and sand in the stomachs. Of 28 stomachs examined, three were well-filled, 10 half-filled, and 15 empty. Johnson and Fielding (1956) raised *P. setiferus* larvae on cultures of algae and copepods, and fed young and adults on ground fish. Others have fed adults a diet of ground fish or shrimp. Pearson (1939) raised postlarvae and juveniles on pieces of shrimp. Attempts at feeding of postlarvae in this laboratory have shown that the young grow better on a mixed diet of algae and *Artemia* nauplii than on either alone, although a pure animal diet produces more rapid growth than a pure plant diet. I have watched postlarvae capture and eat unidentified nauplii in a watch glass. Flint (1956, and personal communication) reported that *P. setiferus* larvae consume and digest blue-green algae, and that larger sizes eat a great diversity of materials including filamentous blue-green algae, lithophytic algae, and diatoms. Forster (1953) has shown that it is nearly impossible to starve caridean shrimp in captivity because they will eat their own feces which contain cultures of ciliates. Mistakidis (1957) has listed the natural food of *Pandalus montagui* in detail. Stomach contents of this prawn varied with locality but consisted of polychaete fragments, gammarids, *Mytilus* larvae, hydroids, algae, and other materials. Reddy (1934) in one of a series of studies on the gastric armature of decapods referred to *Penaeus indicus* as having a "gastric armature . . . more intended for tearing into small pieces its soft prey than for breaking down hard structures as is the case with animals which live on foodstuffs encased in shell and other chitinous envelopes." Reddy found no trace of broken shell or chitinous forms in stomachs of this species, but he did find soft animal forms such as small fishes and worms. Woodburn *et al.* (1957) indicated that *P. duorarum* is omnivorous, and all other evidence indicates that *P. aztecus* and *P. setiferus* are also. It appears that the diet changes between larval and postlarval stages. Omnivorous animals might be attracted to any area rich in food, and in estuaries or the littoral zone of the ocean most areas could afford forage.

Aside from the food supply, Williams (1955a) emphasized the importance of cover in the nursery areas. It would appear that the need to find cover may be complementary to a need for food. Cover may take the form of vegetation, debris-strewn bottom, or the substrate itself. *P. duorarum* can burrow in a coarse substrate, and so long as it can find food on such bottoms it may live there, but in relative absence of food as in the experimental troughs, *P. duorarum* still remains on this type of substrate. On the other hand, *P. setiferus* and *P. aztecus* tend to avoid the coarse substrates and seek cover and food by ranging over and burrowing in softer bottoms. Thus the substrate, aside from its food content, appears to exert an influence on the shrimp.

Beyond a need for cover and capacity to burrow, the respiratory requirements of the species may govern burrowing habits to some extent. When a shrimp has burrowed in the bottom a small hole is sometimes seen in the substrate near the rostrum. This is the site of the inhalant current.[2] It is suggested that pore space in shell-sand would permit more rapid pumping than in pure beach sand or mud. Likewise, the loose peat, largely a submerged mat of decomposing vegetable matter, also has great pore space. All three species concealed themselves best in the loose peat, sometimes burrowing completely below the surface. Likewise, *P. duorarum* burrowed deeply, out of sight, in shell-sand.

[2] A detailed description of the pumping process has been given for an Australian penaeid since this paper went to press by W. Dall, 1958, "Observations on the biology of the greentail prawn *Metapenaeus mastersii* (Haswell) (Crustacea Decapoda: Penaeidae)," Australian J. Mar. Freshw. Res., **9**(1): 111–134.

In another as yet incomplete experiment, *P. aztecus* hid itself completely below the surface in coarse sharp sand. Such behavior indicates that the animals adjust burrowing not only to the ease with which they can enter the ground but also to their respiratory requirements.

Two important environmental factors have not been investigated. Hydrogen-ion concentration of the substrate may influence attraction to a substrate, but no analyses of pH were conducted. Effects of crowding or gregariousness in the tanks or in nature are unknown, although individuals were seen in close proximity to one another when swimming freely, resting on the surface, or when burrowed in the ground.

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# Observations on the Formation and Breakdown of the Oxidized Microzone at the Mud Surface in Lakes[1]

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ABSTRACT

Evidence is presented indicating that the winter thickness of the oxidized microzone at the surface of lake muds may depend upon turbulent displacement of the uppermost sediments into the overlying aerated water, as well as upon the reducing power of the sediments themselves. It is also suggested that this winter oxidized layer may disappear mainly from the surface downward, owing to the greater oxygen consumption there brought about by decomposition of sedimented plankton. Lastly, evidence for a final evolutionary phase of lake sterility, due to development of extremely reducing conditions in the bottom mud, is examined and rejected.

In 1942 Mortimer, in his classic study of the exchange of dissolved substances between mud and water in English lakes, described the existence at the mud surface of an oxidized microzone, which he showed to exert a pronounced influence upon the exchange of substances across the mud-water interface. This oxidized layer he believed to be maintained by molecular diffusion of oxygen into the mud, to a distance depending in winter almost wholly upon reducing power (or oxygen demand) of the sediment in any given lake. However, in the course of studies on Esthwaite Water, the most "eutrophic" of the series examined by Mortimer, the writer has come to believe that the reducing power of the mud is of relatively less importance in determining the winter thickness of the oxidized layer than the degree to which turbulence stirs the mud up from the bottom and into the aerated water column above.

If "the presence of an oxidized microzone throughout the entire year in some lakes, and its disappearance seasonally in the deeper parts of the basin in others, may well be the most important dichotomy in the chemical classification of lakes" (Hutchinson 1957), it would seem of considerable interest to establish the factors controlling its thickness. Evidence for the "turbulent displacement" hypothesis will now be presented, with in addition some observations upon these layers in other lakes, and upon the breakdown of the oxidized layer of surface mud in Esthwaite Water during summer stratification.

## EFFECTS OF TURBULENCE UPON THE MUD SURFACE IN ESTHWAITE WATER

From December 1954 to November 1955 the undisturbed mud surface in the deepest part of Esthwaite Water was examined weekly in four cores taken N, S, E, and W of a fixed buoy with the Jenkin surface mud sampler (Mortimer 1942, Fig. 22). During the first six months a surface layer of rather orange-brown mud could be very clearly and sharply distinguished from the blackish-brown or black mud below, which owed its dark color to precipitated ferrous sulphide. The depth of the orange-brown surface layer, averaged from four points around each core, varied from 6 to 38 mm, averaging about 20 mm. There was not a great deal of change over the whole six months, depth averaging 18 mm in December, and 22 mm in June when the

[1] It is a pleasure to thank Dr. F. R. Hayes, Mr. Byron Reid, Dr. J. W. G. Lund, Dr. Harold Mundie, Miss V. G. Collins, and Dr. C. H. Mortimer for many helpful discussions of these problems. I am also much indebted to Mr. G. J. Thompson and the laboratory staff of the Freshwater Biological Association for collecting the core samples.

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lake was stratified but with oxygen still present in the hypolimnion. In this connection Collins (1956) records that the topmost 20 mm of Esthwaite mud contains an aerobic bacterial flora in winter. It may further be noted that special samples taken at the end of the stratification period, after the surface mud had had a summer in which to consolidate, revealed that the top 15 mm or so of mud were less than half as dense as succeeding 20 mm sections down to 95 mm (dry weight of mud = 0.06 g/cc as against 0.15 g/cc).

If this surface orange-brown layer is the result simply of molecular oxygen diffusion into the mud to a depth depending upon its reducing power, one would expect anaerobic cores to develop such a surface layer upon aeration of the overlying water. To test this hypothesis several cores were taken from Esthwaite Water during September of 1955 and 1957 after the mud surface had become completely reduced and black in color, and these were subsequently aerated in the laboratory without any disturbance of the mud surface. (In 1955 this was accomplished by bubbling air through a U-tube suspended near the bottom of the water column, while in 1957 circulation was provided by running a heating element down one side of the water column in an open core tube, as suggested by F. R. Hayes in a private communication.) Some cores were stored at room temperature, others at about 7 and 12°C, for periods lasting up to four months; but in no case was the orange-brown surface layer characteristic of winter conditions produced. While an orange floc of ferric hydroxide began to accumulate upon the mud surface following the introduction of oxygen, this seldom gave a blanket of more than a few mm thickness, and the mud beneath remained quite black in color. As time went on the orange surface deposit tended to consolidate somewhat, while the mud beneath generally showed little change, except in places where tubificid worms introduced air down their tubes and produced an orange channel into the top 10–20 mm of mud. (In one exceptional case, in a core stored at about 12°C and containing a larger number of tubificid worms than usual, the surface black mud gradually turned brown after about three months due to their activities, but the brown layer so produced was very irregular in depth.) Only when the topmost mud was actually stirred up into the aerated water and redeposited did a thick brown oxidized layer appear over the blackish reduced mud, suggesting that in the lake as in the laboratory turbulent displacement is necessary to its formation. That it cannot be wholly the result of fresh sedimentation is indicated by the studies of Tutin (1955), who records deposition of only about 0.05 mm per week in Windermere over the year 1940–41, and also similar rates in Esthwaite for the period March 12–June 6, 1941 when the two lakes were compared. Moreover, she observes that some of this sediment appears itself to have been swept off the bottom (see later).

At about the time of the 1955 experiments, the effects of the autumn overturn were being followed in the weekly cores. Within a week of its completion a slight (ca 1 mm) surface floc of orange ferric hydroxide was observed. The following week three of the cores showed little change, while the fourth exhibited a thick (5–10 mm) blanket of orange-brown floc. This last core was taken north of the buoy, where the orange-brown layer was most often thickest in winter, and it was inferred that this site was probably a slight depression which tended to collect materials swept up from the mud by turbulence.

A more direct indication of turbulent stirring was observed during the overturn period itself. At an early stage in the breakdown of the thermocline a dense blanket of greyish-green algal filaments (*Melosira italica* subsp. *subarctica*) was observed to accumulate and cover the surface of the mud in the deepest part of the lake for about two weeks. Then, on October 18, a gale combined with heavy rain succeeded in completely overturning the lake, and within 24 hours this blanket was entirely dispersed, and remained so for the fortnight following, after which observations ceased. Lund (1954, 1955) has shown that

*Melosira*, whose filaments (averaging about 0.3 mm long) exhibit a rapid sinking rate whenever the lake stratifies, is frequently swept up from the mud in great quantities, and indeed appears to depend for its existence upon the regular stirring up of the mud surface at overturn, leading to turbulent suspension of the algal filaments during the period of isothermal circulation. Collins (1956) and Mundie (1956) also report phenomena which may be construed as evidence that bacteria and chironomids are swept up from the bottom deposits at the same time.

In 1957 the process of establishing an oxidized surface layer in the mud was followed much farther. Observations began on September 2, when Esthwaite Water was still stratified. At this time the mud was strongly blackened by ferrous sulphide from the surface to an average depth of about 15 mm, below which the color was a more blotchy blackish-brown for 20–30 mm and then a more solid black again beneath. A dense concentration of blue-green algae (*Microcystis* and *Coelosphaerium*) was noticed in the water overlying the mud, and a thin (1–2 mm) band of these green colonies, which were easily visible to the naked eye, was seen at about 5–10 mm beneath the mud surface. This suggested some degree of turbulent disturbance of the mud surface even before the autumn overturn, for it is unlikely that these cells could become stratified under the mud in any other way. It is also improbable that the band could be the result of downward smearing in all four cores, since the top 10–20 mm of deposit is very loose and flocculent, and visible smearing has only been observed in the deeper and more compacted horizons of these cores. Moreover, later examination of vertical sections from frozen cores revealed that these algae did in fact become mixed well into the sediment, thus confirming the conclusions reached earlier from examination of the mud visible through the sides of the core tubes.

On September 10 the bottom water in Esthwaite became aerated again. By the next sampling date (September 16) the upper blackish layer, which on this occasion averaged 17 mm deep in the four cores, was blotched with flocculent orange ferric hydroxide, and the tubificid tubes usually present in these cores were also bright orange with this material. Green algal colonies were also observed to be mixed throughout the loose upper layer. By the following week there was less ferric hydroxide in the surface black mud, suggesting that reduction processes were more than balancing the entry of fresh oxygen. However, by September 24 the lake had become completely isothermal, and on September 30 the surface layer was again a mottled mosaic of black and orange patches in its upper part, with green algal colonies throughout, although it may be remarked that the very bottom of the surface horizon was still fairly solid black with ferrous sulphide.

On October 7 the uppermost loose mud (averaging on this occasion 11 mm deep) was becoming a fairly uniform orange-brown but with flecks of black ferrous sulphide throughout, and, at the very bottom of the layer, a tenuous interrupted band of black ferrous sulphide remained witness to the earlier phase of complete reduction. This state of affairs persisted until early November, when the flocculent surface layer was observed to be almost wholly orange-brown in color, with only scattered flecks of black ferrous sulphide, and no band at the bottom. At this time its thickness averaged about 14 mm.

The mixing of orange flocs of ferric hydroxide, and especially of algal colonies, deep into the uppermost black horizon at the onset of autumn circulation strongly suggests turbulent churning of the surface mud by the overlying aerated water. The observational evidence is squarely against a gradual deepening of the oxidized microzone in response to molecular diffusion of oxygen, and all in favor of sudden turbulent displacements bringing about penetration of oxygen nearly to the bottom of the surface flocculent layer, and also the distribution of algal colonies from the overlying water well into the top 10–20 mm of mud. Another point in favor of this hypothesis is the fact

that tubificid tubes (easily noticed after overturn because of their bright orange sheaths extending from above the mud well down into the black horizons of ferrous sulphide) often became truncated at the boundary between orange-brown and black mud, so that only the deeper part remained.

These tubificid worms must disturb the sediment in Esthwaite Water by working the surface layers and casting their faeces into the overlying water, but storage experiments in the laboratory have not shown their activities to be very significant. Nor, according to the laboratory observation, is the production of gas bubbles deep in the anaerobic layers of mud very important in this connection although it occasionally brings about some disturbance in peaty bottom deposits.

A final point with regard to Esthwaite Water may be made from Mortimer's observation that after overturn in 1940 "the thickness of the oxidized layer was subject to considerable fluctuations. During a calm spell in December it consisted only of a surface scum containing ferric hydroxide, and it was again almost destroyed during stagnation under ice from 3 January to 15 February 1941." Since oxygen concentrations just above the mud rose steadily throughout December it seems strange that the oxidized microzone should almost disappear, *unless* we assume that the calm weather, by preventing the mud from being occasionally mixed with the overlying aerated water, was responsible for the phenomenon. We may explain the near-destruction of the oxidized layer during stagnation under ice in a similar way, although in this case oxygen data are lacking and we have to rely on the high redox potentials (0.5 V) 10 mm above the mud as evidence for the presence of well-aerated water there.

### EVIDENCE FROM OTHER LAKES

An indication of the influence of turbulence upon the bottom deposits in Windermere is given by Tutin (1955) in her paper on the cycle of sedimentation in the North Basin. She observed a marked decrease in sedimentation during August and September 1941, when stratification was most stable, followed by a sharp rise in early October to levels comparable with those maintained during the entire period of isothermal circulation. Evidence is provided that this October rise was due to the occurrence on September 30 of the first autumn gale, which stirred up material from the bottom above the thermocline and redistributed it partly to the deeper waters. She further points out that while freshly collected sediment is usually olive-brown in color, and only changes to dark brown and more compacted flocculi upon storage, on several occasions (especially at overturn) the fresh sediments had this darker and more "mature" appearance, suggesting that they had been swept off the bottom and redeposited in the sediment traps above.

Another piece of evidence suggesting turbulent displacement of the mud surface in this lake is Mortimer's statement that the thickness of the oxidized microzone was doubled after the autumn overturn in 1940. Since oxygen concentration just above the mud was fairly high before the lake became isothermal (about 9 mg/L), and only rose by a little over 20 per cent (to 11 mg/L), it seems more reasonable to suppose that turbulent displacement was the agent responsible for this sudden descent of the oxidation-reduction interface.

Yet a further finding of Mortimer's may well be explicable on the same grounds. In measuring electrical conductivity (an indication of total dissolved ions) down two series of mud cores from Windermere North Basin, one taken at the end of summer stratification (A), and the other at the end of the circulation period (B), he recorded distinctly lower values in the latter case at comparable depths in the cores. The two curves are shown in Figure 1, from which it is evident that they are very similar in appearance. Indeed, it might easily be imagined that the curve for the end of the circulation period (B) represents the earlier gradient (A) somewhat less steep, and displaced slightly downward, so that its origin lies well within the mud rather than near its surface. Such a downward displacement could well result from turbulent disturbance

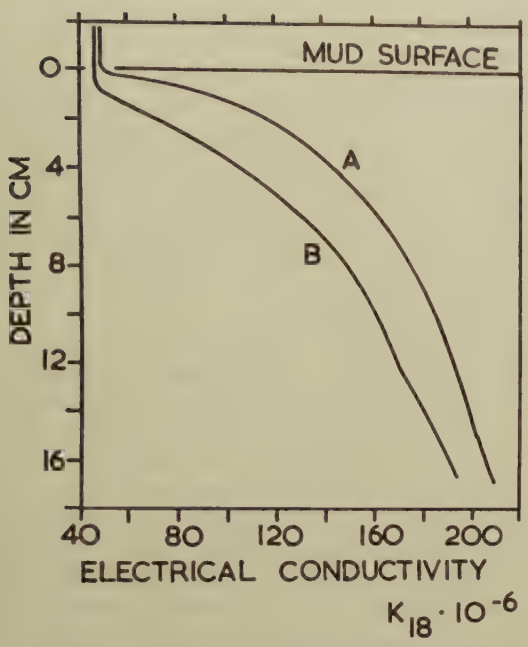


FIG. 1. The relation between electrical conductivity and depth in surface mud cores from Windermere North Basin, (A) at the end of stratification, and (B) at the end of isothermal circulation (after Mortimer 1942).

of the mud surface, and the fact that in curve (B) the conductivity of the uppermost mud is the same as that in the water column above strongly suggests that it has actually been mixed with the overlying water and in this way has lost its excess of ions diffusing from below.

So far we have dealt with both the deepest and the shallowest of the five bodies of water investigated by Mortimer, and it remains to see whether any evidence for turbulent displacement can be gathered from the lakes as a group. Two suggestive features of Mortimer's earlier work deserve consideration in this connection.

The first is the pattern of redox potential distribution in the muds, which is illustrated in Figure 2 for Esthwaite Water and Ennerdale Water, which give the two extremes of winter redox profile, and for Crummock Water, from which the only summer profile was obtained. The most interesting feature of the winter curves is that they *do not show* the gradual decline of potential from the mud surface which one would expect if oxygen penetration into the mud were due solely to molecular diffusion. On the other hand, the presence of potentials well within the mud which are just as high as those in the overlying water argues strongly that there must be some turbulent mixing involved, leading to the penetration of the overlying aerated water right into the uppermost horizons of the mud. If the above argument is correct, we can then estimate roughly the depth of effective turbulent displacement as being the depth to which redox potentials as high as those in the water (approximately 0.5 V) are found in the mud. The values thus obtained (very crudely, from Mortimer's Fig. 43) are as

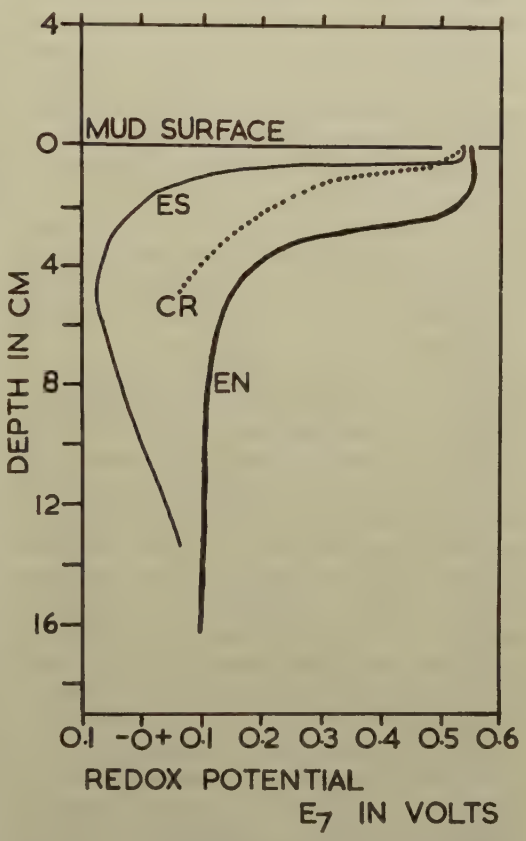


FIG. 2. The relation between redox potential and depth in surface mud cores from Esthwaite Water (ES) and Ennerdale Water (EN) at the end of isothermal circulation, and Crummock Water (CR) at the end of stratification (after Mortimer 1942).

follows: Crummock Water 4 mm, Esthwaite Water 5 mm, Windermere North Basin 6 mm, Windermere South Basin 11 mm, and Ennerdale Water 20 mm. Of these, the value for Crummock Water represents late summer conditions, and so is not comparable to the rest. However, the Crummock *redox/depth* gradient is of great interest for this very reason, in that it alone of the five curves exhibits the gradual decline of potential from the mud surface which is to be expected if only molecular diffusion of oxygen is involved; and it alone represents a time when turbulent disturbance of the mud might be expected to be minimal.

In connection with the depths of turbulent stirring estimated above, it may be remarked that the further distance into the mud between the 0.5 V and the 0.2 V isovolt may be taken as a rough indication of the relative effectiveness of molecular oxygen diffusion in aerating the various lake muds. For this property the respective values are: Esthwaite 2 mm, Windermere North Basin 5 mm, Windermere South Basin 6 mm, Crummock Water 18 mm, and Ennerdale Water 20 mm. The trophic series obtained by Mortimer is thus seen to be maintained, although the method of measurement is changed.

The second feature of Mortimer's results bearing on the problem of turbulent mud displacement is his finding that the exponential increase of electrical conductivity downward, which he noted as characteristic of all the lake muds (see his Fig. 46), fails to hold near the mud surface. Mortimer explains this as being due to ion adsorption in the oxidized layer, but this conclusion is open to question (Gorham *in preparation*), and turbulent disturbance of the oxidized microzone may well provide an alternative explanation.

A last point to be noted about these redox curves is that in the middle horizons around 50 mm the Ennerdale potential is much less than the others (see Mortimer's Fig. 33). This is probably connected with the virtual absence from Ennerdale cores of any black staining by ferrous sulphide, a compound found only in strongly reducing environments, and observable in some quantity in all the other cores, especially in Esthwaite Water.

A final piece of evidence for turbulent stirring of the mud surface as a general phenomenon may be found in Lund's (1954) report that the life cycle of *Melosira italica subarctica*, common in at least seven of the larger lakes in the English Lake District, depends for its existence upon re-suspension from the bottom deposits, to which it sinks rapidly in calm weather.

From the observations and experiments described above, it seems inescapable that turbulent displacement plays an important role in establishing and determining the winter thickness of the oxidized microzone at the surface of the mud in Esthwaite Water, and probably in the other lakes as well. If so, this property must be controlled by a complex of interacting factors: some morphometric and affecting turbulence (*e.g.*, basin size, shape, and exposure), others edaphic and affecting oxygen diffusion (*e.g.*, texture, density, and permeability), and yet others biological, and influencing the reducing power of the mud (*e.g.*, the nature and amounts of organic residues produced in the lake and entering it from outside, and also the nature and amounts of the organisms inhabiting the mud). In the light of this complexity, the correlation between thickness of the oxidized microzone in winter and areal rate of oxygen absorption in summer seems most remarkable, and deserving of further investigation. It is hoped that this correlation may be re-examined, together with the factors controlling turbulence at the mud surface, in the near future, when the underwater camera and current meter now being constructed in this laboratory should prove of great value.

## BREAKDOWN OF THE OXIDIZED SURFACE LAYER

The thickness of the oxidized microzone was believed by Mortimer to decrease from below upward as thermal stratification progressed. However, observational evidence from Esthwaite Water again suggests otherwise. During 1955 in Esthwaite Water, thermal stratification began in April, and oxygen stratification by the beginning of

May. However, the boundary of the upper brown mud at about 22 mm remained very clear until well on into June. By June 15 a slight orange floc was observed to develop in bottom water samples on standing for a few days in the air—evidence that ferrous iron was diffusing out of the mud surface into the water above, which still contained considerable amounts of oxygen. It was also noticed on this date that a great deal of *Melosira* had fallen onto the mud surface, and in the cores of the following week a thin black layer had formed at the mud surface beneath this algal mat. Presumably ferrous sulphide had precipitated there due to the intensity of algal decay.

This was the last week that *Hydra* appeared on the mud surface. During the winter a few were observed in most weeks, and occasionally half a dozen or so occurred in a single core, but during May they were seldom seen. On June 28, when more *Melosira* had fallen together with a mass of dead *Daphnia* from the zooplankton peak a short time before, the surface black layer was found again, and some flecks of black had begun to appear in the brown mud beneath, whose lower boundary was becoming difficult to distinguish. A test of the overlying water in these cores with dithizone gave no coloration, but on July 5 a pale pink tinge characteristic of manganese was noticed, and by July 12 this color had become much stronger. On July 19 in mud-water cores that had stood overnight a heavy orange floc appeared at the mud surface, which is evidence of intense ferrous iron mobilization there at this time. Meanwhile the brown surface layer became much more spotted with black ferrous sulphide, especially toward the surface; and in mid-July, when the bottom water had become completely anaerobic (modified Winkler, V. G. Collins, private communication), the boundary of the brown layer was no longer distinguishable.

These black flecks presumably represent local centers of intense reduction, most likely around organic debris; and the heterogeneity thus revealed within a given level probably accounts for the great difficulty experienced by Miss V. G. Collins (private communication) in getting reproducible redox potentials in the upper layers of summer cores from Esthwaite Water. It may well be that turbulent re-distribution of the upper mud smooths the winter *potential/depth* curves shown in Mortimer's Fig. 43, by mixing and aerating this variably reducing layer of surface mud.

By early August a layer of 5–10 mm of very black mud had accumulated at the surface in two cores, and in early September an even thicker black layer of about 10–20 mm developed in all cores. In addition it was noted that much less orange floc precipitated when the core water was left open to the air, suggesting that most of the ferrous iron was by that time precipitated as ferrous sulfide and less easily diffusible.

These results indicate that reduction of the winter oxidized layer does not proceed mainly from the bottom upward, but from numerous sites within the layer and particularly at the mud surface, where the presence of abundant organic remains following the peaks of phytoplankton and zooplankton provides a stimulus for bacterial oxygen consumption.

A last point to be remarked is the possibility, mentioned by Mortimer, that intensive reduction of bottom mud may lead to a phase of lake sterility, associated with precipitation of most of the iron as ferrous sulfide. This idea appears to be taken over from Misra (1938), whose studies of small local areas along the shores of Esthwaite Water and Windermere revealed occasional bare patches of mud with a relatively high ignition loss. These were claimed to be deficient in adsorbed bases but rich in adsorbed hydrogen ions, so that the base saturation of the soil colloids was very low (5–10 per cent). Since these same muds were reported as having pH values of around 6, it seems most unlikely that the base deficiencies reported are real. The present writer (Gorham 1953) has obtained much higher base-saturation percentages (70 per cent or more) from both black and brown patches of bare mud in the same general area, and in his opinion Dr. Misra's method for exchangeable hydrogen is at fault. The bareness may well reflect not sterility but

the activities of swans, boaters, and even limnologists, all easily able to root up large patches of *Littorella*, *Isoetes*, and other vegetation from these soft littoral muds. Evidence against the sterility of these muds is also to be found in their possession of abundant surface growths of algae (Lund, private communication). It may therefore be concluded that evidence is lacking for a terminal evolutionary stage of lake sterility, consequent upon a phase of rapid organic production and development of intensely reducing conditions in the lake bottom. Certainly the writer cannot call to mind any case of lake sterility following upon natural eutrophication, though pollution might bring about such a result.

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# Lake Water and Sediment

## I. Characteristics and Water Chemistry of Some Canadian East Coast Lakes[1]

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ABSTRACT

Sixteen lakes are described, varying in geology and all but two of low productivity, and including three acid bog types. A method is described for indirect estimation of the sum of Na and K. In lakes generally, low pH is related to low conductivity, but in these coastal lakes the Na in ocean spray keeps up the conductivity even in very acid waters. At equilibrium the inorganic P in solution is 2–3 ppb and represents a residual soluble fraction, independent of productivity and pH. Total P is 10–15 ppb and the concentration is not related to productivity. There is an annual cycle of inorganic P with a winter maximum, spring decline, and summer minimum. Methyl orange alkalinity varies directly with the sum of Ca and Mg and with either of the ions separately. The scatter in the regression of alkalinity versus Mg is greater than that of alkalinity versus Ca. There is a reduction of per cent organic material in the sediments directly related to increasing alkalinity. The cause is attributed to greater bacterial activity as the pH goes up.

These papers are in continuation of studies related to the productivity of some east coast Canadian lakes. The lakes selected exhibit considerable variety of type and geology, as shown by their map locations (Fig. 1). From the work of M. W. Smith the capacity of many of the lakes to support fish is known, providing a standard by which to judge other estimates.

The following notes on the lakes will supplement Figure 1 and Table 1.

Lakes 1, 2, and 3 are located near Halifax in forbidding granite country. No. 1 is a clearwater primitive, No. 2 an extreme acid bog type, and No. 3 moderately acid bog.

Lakes 4, 5, and 6 are near Yarmouth in a quartzite-slate formation, No. 4 being an acid bog type. Their quality indices, based on fish, are respectively 0.20, 0.53, and 0.98, where 1.0 would be average (Hayes 1957).

Lakes 7 to 11 are scattered over Nova Scotia. Nos. 7 and 8 are not far apart in a sandstone-shale conglomerate. The drainage area of No. 8 supports marginal farming, and the lake has a quality index of 0.36. Grand Lake, No. 9, is the largest and deepest of the group and known for its landlocked salmon. It drains quartzite-slate from the south, and a conglomerate of shale, sandstone, and lime from the north where farms are situated. The same conglomerate surrounds Lily Lake, No. 10, also in a farming area. The water is too warm for trout. Lake 11 is in altered sediment and igneous rocks. Its quality index is 0.87.

Lakes 12, 13, and 14 are close together near St. Andrews, in a granite area. Their quality indices are low, being respectively 0.28, 0.31, and 0.09.

Finally, lakes 15 and 16 are in the best trout area of the region, where up to 50 lbs per acre are taken annually. Like practically all ponds in Prince Edward Island, they are artificial, retained by mill dams a century or more old. Trout are plentiful not only because of good drainage but because the water keeps cool all summer and competitors have not crossed from the mainland. The quality indices are 6.2 and 5.5. The area is one of sandstone, shale, and conglomerate.

### METHODS

The writers and colleagues have been conducting periodic summer analyses on these lakes, for up to a decade on some. Certain techniques have been changed, per-

[1] Acknowledgement is made of financial support by the Nova Scotia Research Foundation and National Research Council of Canada. We thank a dozen students who participated, and especially James Rose.

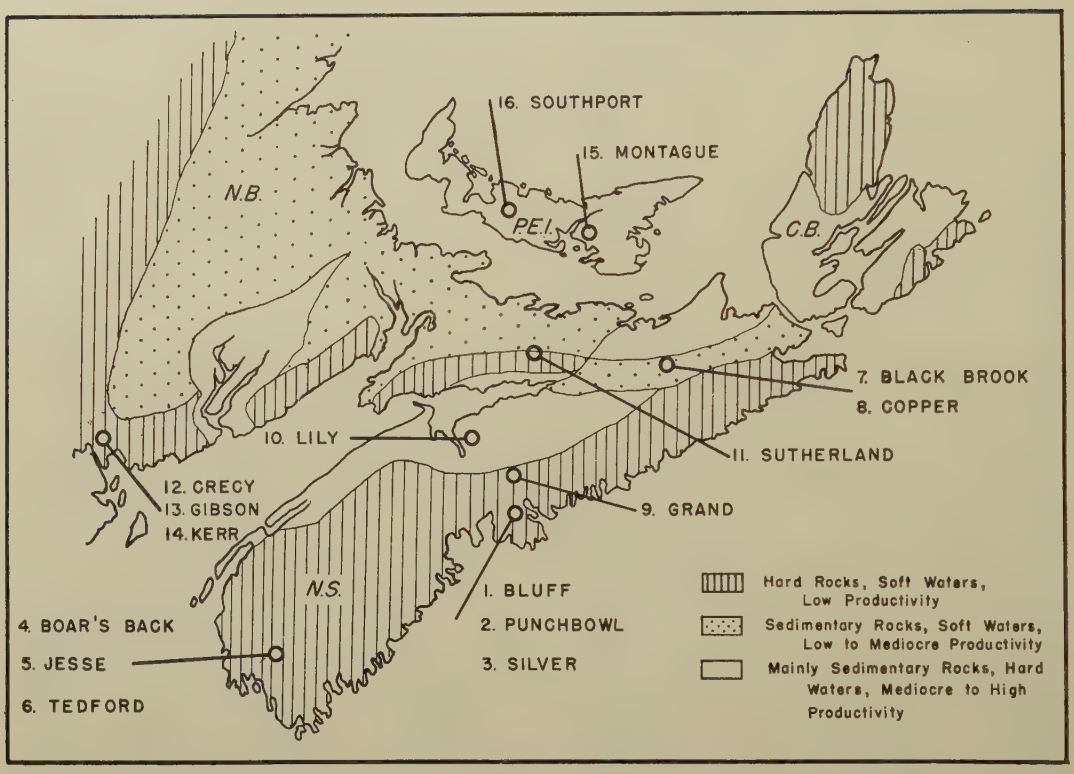


FIG. 1. Location of lakes studied, and indication of basic geological formations in the area, the latter from Smith (1957). Abbreviated area names refer to Nova Scotia, New Brunswick, Prince Edward Island, and Cape Breton Island.

mitting comparisons of earlier and later work. Ten lakes can be compared with previous work by M. W. Smith (1938, 1952, 1954); five with Gorham's (1957a) winter analyses of water; three others with Leverin (1947); and one (a Mendota water sample) with data in several papers by Juday and others. Comments which follow on the accuracy of certain methods are based on a study of these parallel analyses.

Hydrogen-ion concentration was measured with a glass electrode. In our poorly buffered lakes the drift to an end point might take a minute or more. A hurried reading would tend to retain the pH of the buffer or to approximate 5.7, which is the pH of distilled water in equilibrium with atmospheric $CO_2$, often used as a preliminary rinse. Results reported are those following shaking, which generally made little difference, or at most increased the pH by 0.2 unit. In winter the change may be greater; *e.g.*, Gorham gives one lake sample in which the pH increased by 0.8 on shaking. In general pH seems to have little stability in unbuffered waters.

The conductivity technique has been described (Hayes and Beckett 1956). Results from one summer to another and from winter to summer are generally quite close. The procedure is regarded as satisfactory.

Color was determined from optical density measurements, calibrated to a platinum-cobalt standard. A Lumetron colorimeter was used with a 420 filter. The water was allowed to settle for 24 hr in the laboratory and decanted before measurement. Color did not vary much from summer to summer, nor from summer to winter in clear lakes, although two bog lakes had winter values only one-third and one-fifth those of summer. Thus in bog lakes such as our Punchbowl, Boar's Back, or Silver, color is due to swamp drainage and is evidence of low pro-

TABLE 1. *Location, dimensions, and chemical analyses of summer surface waters of 16 east coast Canadian lakes*

On lakes 12, 13, and 14, Na + K values in parentheses are from Leverin, and total phosphorus from Smith. As all results are averages of several analyses, the exact estimated value from Na + K will not necessarily be obtained by use of the procedure outlined in the text.

| Lake number | Name | Map position | | Area ha | Mean depth m | Stratified | Pt-Co color ppm | pH | M.O. alk. as ppm $CaCO_3$ | Cond. 20° megambos | Cations—ppm | | | | | Phosphorus—ppb | | Dredged sediment | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | W | N | | | | | | | | Ca | Mg | Na | K | Na + K est. | Total | Organic | % dry wt. | % org. in dry wt. |
| 1 | Bluff | 63°39′ | 44°33′ | 4.0 | 3.0 | No | 2 | 5.3 | 7.4 | 35 | 1.4 | 0.6 | 4.3 | 0.33 | 4.7 | 6.6 | 5.0 | 7.9 | 37.6 |
| 2 | Punchbowl | 63°48′ | 44°41′ | 0.3 | 4.9 | Yes | 238 | 5.2 | 6.3 | 35 | 1.4 | 0.7 | 3.5 | 0.34 | 4.5 | 33.7 | 28.4 | 7.9 | 52.7 |
| 3 | Silver | 63°39′ | 44°33′ | 1.2 | 1.8 | Yes | 140 | 5.2 | 6.5 | 40 | 1.3 | 0.7 | 3.6 | 0.30 | 5.9 | 22.5 | 20.6 | 7.8 | 50.4 |
| 4 | Boar's Back | 65°57′ | 44°09′ | 23. | 2.6 | No | 163 | 4.7 | 5.7 | 41 | 1.3 | 1.0 | | | 4.0 | | | 9.1 | 33.9 |
| 5 | Jesse | 66°01′ | 44°02′ | 18. | 2.4 | No | 21 | 6.5 | 8.5 | 49 | 2.2 | 1.3 | | | 7.5 | | | 14.3 | 17.9 |
| 6 | Tedford | 66°01′ | 44°06′ | 21. | 2.4 | No | 6 | 6.6 | 7.7 | 44 | 2.4 | 1.1 | | | 5.7 | | | 10.9 | 21.6 |
| 7 | Black Brook | 62°10′ | 45°26′ | 26. | 6.4 | Yes | 64 | 6.8 | 11.3 | 35 | 3.1 | 0.9 | | | 2.9 | 8.4 | | 12.4 | 32.4 |
| 8 | Copper | 61°59′ | 45°24′ | 22. | 5.6 | Yes | 18 | 7.3 | 14.4 | 47 | 4.8 | 0.8 | 3.4 | 0.47 | 3.8 | 12.4 | 10.1 | 15.6 | 17.9 |
| 9 | Grand | 63°36′ | 44°55′ | 1740. | 15.1 | Yes | 21 | 6.4 | 5.0 | 37 | 3.6 | 0.4 | 2.7 | 0.26 | 3.8 | 11.8 | 9.2 | 13.3 | 21.0 |
| 10 | Lily | 64°06′ | 45°05′ | 37. | 1.7 | No | 75 | 6.5 | 9.4 | 32 | 2.5 | 0.7 | 2.9 | 0.67 | 3.4 | 18.4 | 15.0 | 8.0 | 37.4 |
| 11 | Sutherland | 63°41′ | 45°31′ | 41. | 2.2 | No | 13 | 7.0 | 10.4 | 27 | 2.8 | 0.2 | | | 1.7 | 10.9 | | 15.2 | 18.0 |
| 12 | Crecy | 67°01′ | 45°14′ | 20. | 2.4 | No | 10 | 6.7 | 8.4 | 30 | 3.6 | 0.2 | (3.6) | | 2.3 | (14.0) | | 14.9 | 23.7 |
| 13 | Gibson | 67°05′ | 45°10′ | 24. | 4.0 | No | 19 | 6.7 | 11.6 | 34 | 4.6 | 0.3 | (3.9) | | 1.8 | (13.0) | | 5.3 | 39.8 |
| 14 | Kerr | 67°02′ | 45°13′ | 73. | 4.7 | Yes | 18 | 6.6 | 9.2 | 29 | 3.5 | 0.5 | (2.4) | | 1.4 | ( 9.3) | | 5.5 | 33.6 |
| 15 | Montague | 62°40′ | 46°09′ | 9.3 | 2.4 | No | 12 | 8.3 | 55.1 | 148 | 25.0 | 4.0 | | | | 65.8 | 9.6 | 19.8 | 13.9 |
| 16 | Southport | 63°06′ | 46°13′ | 1.0 | 1.3 | No | 35 | 8.9 | 50.4 | 161 | 21.3 | 3.6 | 5.9 | 1.52 | 3.5 | 13.9 | 10.8 | 17.0 | 14.1 |

ductivity. Elsewhere there are productive clear-water lakes in which the cause of color is phytoplankton and here the depth of color may be related to productivity (Juday and Birge 1933).

Alkalinity expressed as ppm $CaCO_3$, was measured by titration with screened methyl orange as in "Standard Methods." Results from year to year show negligible variation. Gorham, using a quite different method reports zero readings automatically at pH of 5.7 or less. In lakes 12, 13, and 14 Leverin, using a methyl red titration, gives values of 0, 0, and 2.5, where we get 8.4, 9.2, and 11.6. The differences are considerable. From a plot of alkalinity against the sum of Ca and Mg (hardness), using data of various authors, the M.O. results fall closer to the general regression line than other kinds, hence appear worthy of retention.

Calcium was formerly determined on a Perkin-Elmer flame photometer, for which the dilute waters had to be evaporated to $\frac{1}{10}$ vol. In 1957 the versenate titration of Heron and Mackereth (1955) was adopted. This was satisfactory for clear waters but did not give a very good end point with colored bog waters. On our soft-water lakes the 1957 Ca results were about 10 per cent above earlier ones, the cause being unknown, possibly loss in evaporating the earlier samples.

Magnesium was formerly done by the colorimetric titan yellow method on the Lumetron, a temperamental test. In 1957 the versenate titration was adopted. The newer results on local lakes were the same as the older. Differences from Gorham's winter results were small and without a trend.

Sodium and potassium were measured on the flame photometer after reducing the lake water to $\frac{1}{10}$ vol. On three lakes compared, the winter results of Gorham are about 20 per cent above ours, possibly a real difference due to ocean spray in storms.

The sum of Na and K can be estimated as follows without having to use a flame photometer. First, the specific conductivity is divided by 2 to approximate anions or, in

this use, cations. Where the pH is less than 5.5, a subtraction for conductivity due to hydrogen ions is made. The value to be subtracted at each pH is given by Sjörs (1950, p. 217). Next subtract the conductivity due to Ca and to Mg, as obtained from the relationship:

$$\text{cond. due to ion} = \frac{\text{equiv. cond.} \times \text{mass as ppm}}{\text{equiv. wt.}}$$

The equivalent conductivity for Ca is 54 and for Mg is 50.5. What is left is the residual conductivity due to Na + K. The equivalent conductivities of Na and K, respectively, are 46 and 68. Assume the ions are distributed 8 Na to 1 K. Then

$$\text{Na + K ppm} = \frac{8}{9}\text{ of }\frac{23}{46} \times \text{res. cond.} + \frac{1}{9}\text{ of }\frac{39.1}{68} \times \text{res. cond.}$$

This simplifies to

$$\text{Res. cond.} \times 0.508 = \text{Na + K in ppm.}$$

The assumed ratio of 8 to 1 for Na to K is reasonable for our own lakes and as good a value as any for other regions, as Table 2 shows. Actually the ratio is of little importance to accuracy, since the difference in final result between a 20:1 and 1.5:1 ratio (the limits of Table 2) is only 3 per cent. What Table 2 does do is to warn against attempts to separate Na and K concentrations by this short method.

TABLE 2. *Sodium and potassium values for lakes in several areas*

| Area | Reference | Number lakes | ppm Na | ppm K | Ratio Na:K |
|---|---|---|---|---|---|
| Halifax, N. S. | Tab. 1, and Gorham (1957a) | 21 | 3.97 | 0.46 | 8.7 |
| Other N. S. | Tab. 1 | 3 | 3.00 | 0.47 | 6.5 |
| Prince Edward Island | Tab. 1 | 1 | 5.86 | 1.52 | 3.9 |
| Cheshire, Eng. | Gorham (1957b) | 7 | 0.75 | 0.11 | 6.8 |
| Shropshire, Eng. | Gorham (1957c) | 13 | 9.55 | 6.76 | 1.4 |
| Western Ireland | Gorham (1957d) | 7 | 9.18 | 0.49 | 18.9 |
| Scotland, granite drainage | Gorham (1957e) | 7 | 1.97 | 0.26 | 7.7 |
| Scotland, Moine series | Gorham (1957e) | 10 | 5.59 | 0.75 | 7.5 |
| Uppland Dist., Sweden | Data of Lohammar (1938), cited from Rodhe (1949) | 21 | | | 3.6 |
| Dalarna Dist., Sweden, (excl. seepage. No. of lakes approx.) | Data of Lohammar (1938), cited from Gorham (1955) | 50 | | | 3.5 |

On seven lakes we have Na + K both directly and via the conductivity method. The two series do not differ significantly and there is a two-to-one chance that the methods will read within 20 per cent on a given lake. The final error, being compounded of subtractions, might become greater in productive regions where there was a great deal of Ca in proportion to the monovalent bases. Thus, attempts to apply the method to two of three Wisconsin lakes, high in Ca, gave negative values for Na + K. A small deviation from the accepted equivalent conductivity of Ca would also be important in Ca-rich lakes.

Phosphorus was determined by the stannous chloride method with Lumetron colorimeter and 650 filter. Inorganic phosphate was done directly including lake water in the reagent blank; total phosphate was measured after evaporation and ashing with perchloric acid.

Sediment analyses were ordinarily made on dredge samples and represent the top few cm. The samples were dried at room temperature for storage and at about 90°C for water content estimates. Ashing was at about 400 to 500°C.

Chemical analyses of sediment have been made but are not presented here because the analytical values obtained for Na, Ca, K, and P depended on the method used. Wet

TABLE 3. *Effect of ashing method on lake sediment analysis*

Dry ashing gave lower values in practically all tests. Dry ashing was at 400° to 500°C followed by extraction with hot dilute HCl. Wet ashing was with nitric followed by perchloric acid.

| Number | Lake | Dry ash as % of wet ash | | | |
|---|---|---|---|---|---|
| | | Na | Ca | K | P |
| 1 | Bluff | | | | 50 |
| 2 | Punchbowl | 70 | 120 | 9 | 60 |
| 8 | Copper | 50 | 100 | 7 | 10 |
| 9 | Grand | 40 | 30 | 9 | 20 |
| 10 | Lily | 20 | 35 | 7 | 30 |

ashing with perchloric acid gave results up to 10 times as high as the dry ashing technique followed by extraction with hot HCl. It may be that dry ashing liberates the minerals that are or have been brought into solution by weathering, while wet ashing breaks up particles of rock not hitherto dissolved. If this is so, a limnologist might prefer dry ashing and a geologist the perchloric digestion. Comparisons of wet and dry ashing which are available on five lakes are given in Table 3.

## DISCUSSION

Table 1 gives analyses on 16 lakes to be discussed in later papers. Analyses which have been made on several additional lakes near Halifax will be presented only as points on graphs. Three Wisconsin lake water samples have been examined and will be cited later. When the east coast lakes are compared with other series, *e.g.*, in Wisconsin (Juday *et al.* 1941), they appear, by conventional standards, to be of low productivity, except for the two Prince Edward Island ponds. Figure 2 shows this, being a plot of two qualities generally associated with productivity. The upper right quadrant is occupied by Wisconsin lakes. Our two P.E.I. ponds are below center and the remaining east coast lakes at the bottom. The regressions of M.O. alkalinity on Ca or Mg alone are like Figure 2, but Mg exhibits considerably more scatter.

A peculiarity of the east coast waters is the failure of conductivity to continue its decline with pH (Fig. 3). In this they contrast with Wisconsin waters. Conductivity

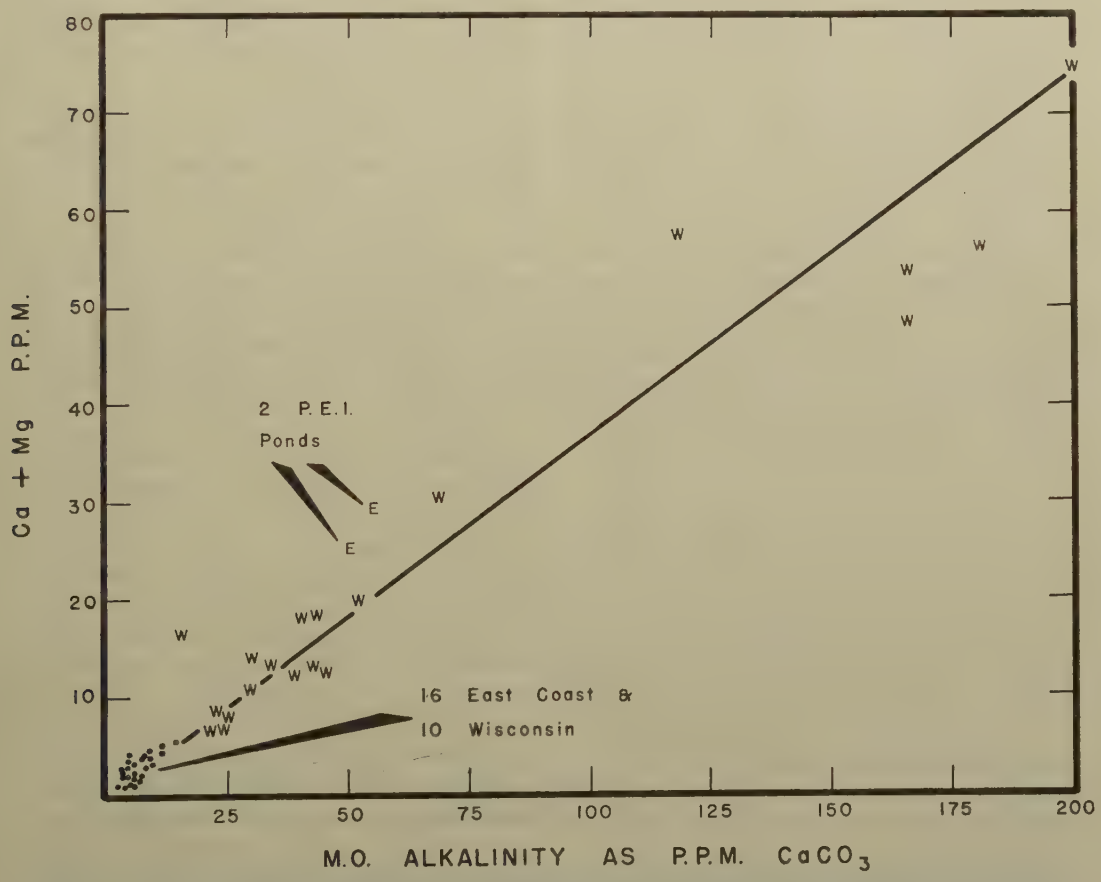


FIG. 2. Plot of methyl orange alkalinity against Ca + Mg to show that on these two standards, commonly associated with productivity, the Canadian east coast lakes are low, except for two Prince Edward Island ponds. Points marked *W* are Wisconsin lakes, chiefly from Juday *et al.* (1941).

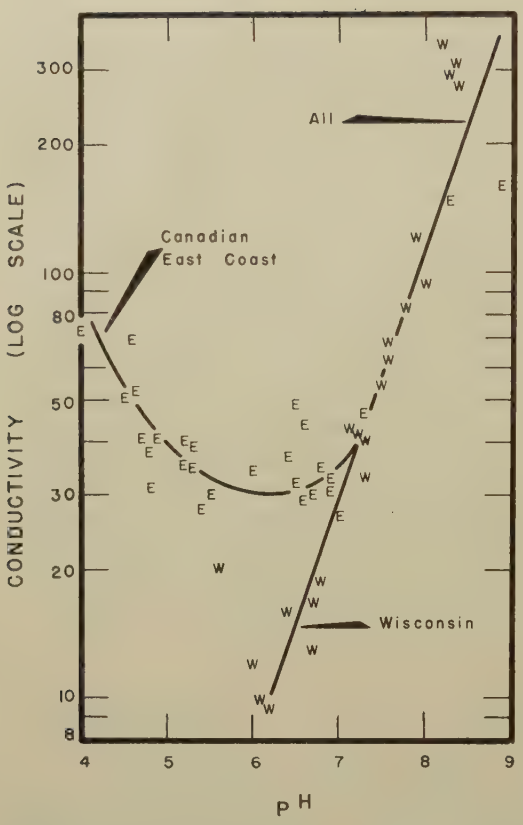


FIG. 3. Plot of conductivity at 20° versus pH. In Wisconsin lakes conductivity continues to decline with increasing acidity. Evidently the Ca, Mg, and bicarbonate which determine pH are the main ions. In the east coast lakes, other minerals, notably NaCl, which are unconnected with pH are present in amounts which hold up the conductivity even at acid levels. A further contribution to conductivity under acid conditions is made by hydrogen ions themselves.

is generally determined largely by Ca and bicarbonate and declines with them, as does pH. In these eastern lakes, however, the conductivity minimum is at pH 6 below which it rises again. This is partly due to H ions, as already mentioned, and partly to sodium chloride, carried in on sea breezes. Probably inland lakes do not have any corresponding delivery of NaCl. It is interesting that the most acid lakes, with their enhanced conductivity due in part to NaCl, were observations of Gorham in winter, when storms would be maximal. The same result as Figure 3 is seen when a plot is made of methyl orange alkalinity against conductivity. However, when a graph is made of log Ca + Mg versus pH, the Canadian lakes flatten below pH 6, but do not turn up. They level off at about the same minimum as Wisconsin lakes, when the sum of Ca and Mg is about 2 ± 0.5 ppm. This may be taken either as the residuum extractable from the rocks under acid conditions, or alternatively as the contribution delivered from the air via dust and rain.

A great many analyses of phosphorus have been made, as this element was once thought to be an indicator of productivity. Table 1 however shows high total P for the acid bog lakes 2 and 3, presumably due to humus carried in from the surrounding swamps. At the bottom, our productive ponds 15 and 16 vary considerably in total P. In these ponds, which drain good agricultural country, M. W. Smith (priv. comm.) found temporary very high P values following rain. Thus the sampling error in productive regions could be large.

The well-known liberation of inorganic P from bottom mud where oxygen is lacking has been observed in stratified lakes 2, 3, and 8, the maximum being 128 ppb in lake 2. Only the lowest meter or so is affected, and the released P if dispersed through the whole water mass would scarcely have a perceptible effect on the concentration. At equilibrium the inorganic phosphorus represents about one-fifth of the total, and is of the order of 2 or 3 ppb. This is probably the residual soluble fraction and is independent of productivity or pH. Being a very low concentration, indeed, it might come from so-called insoluble compounds such as ferric phosphate. The organic part in solution is also small, 10 or 15 ppb, and is maintained in equilibrium with the main store in plant bodies, bacteria, etc. It does not appear to be a measure of productivity, but is rather a transfer unit, like the size of a spoon used to move food from plate to mouth.

Turning to the sediments, Table 1 shows that lakes 15 and 16 which have the largest dry fraction also have the lowest organic part, as is also regionally true, *e.g.*, compare lakes 13 and 14 with 12. This is not very surprising, being merely an indication that

silica, etc. packs better than organic material. The source of high organic content is evidently swamp drainage; thus the highly colored lakes 2 and 3 have higher values than has 1, and number 4 a higher value than have 5 and 6.

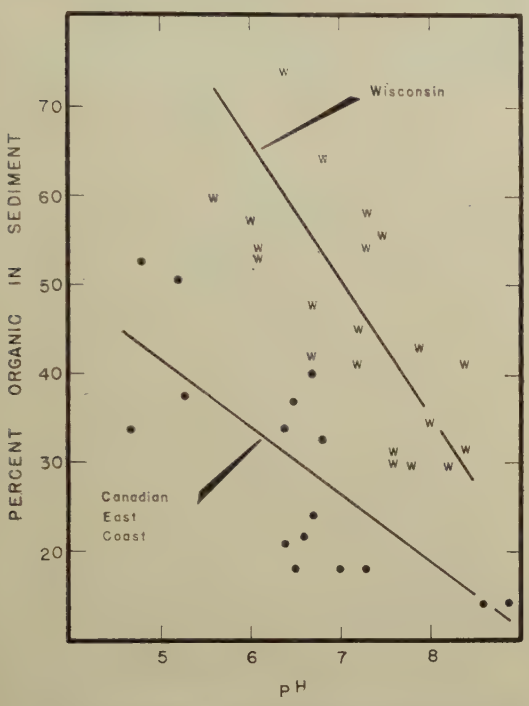


FIG. 4. Relation of pH to the organic content of the sediment. Lakes marked *W* are in Wisconsin (Juday *et al.* 1941). Solid circles are eastern Canadian lakes.

The stimulating effect of alkalinity on microbial activity is shown by the reduction of per cent organic sediment at higher pH levels (Fig. 4). Even though masked by regional differences the slope is apparent. Wisconsin lakes included for comparison show the same trend, although they have a generally higher organic content.

Our productive examples (P.E.I. ponds) are shallow and unstratified, so that bacterial oxidation on bottom sediments will be maximal. In other parts of the world, *e.g.*, in the Alps, productive lakes often have a large hypolimnion with consequent oxygen depletion in the depths. Bacteria could not act effectively on dead material falling through the reduced water or at the reduced mud surface. Hence a large per cent of organic matter might be left in the sediment, even when a lake had high productivity. Indeed, if bacterial decomposition is virtually stopped, a productive lake might have more organic material in its sediment than an unproductive one, as has been reported.

In lakes 2, 8, and 9, the variations in Na, K, Ca, and P have been followed during a year. Samples were taken both above and below the thermocline. The first three elements merit little discussion. There were ups and downs but no seasonal pattern that

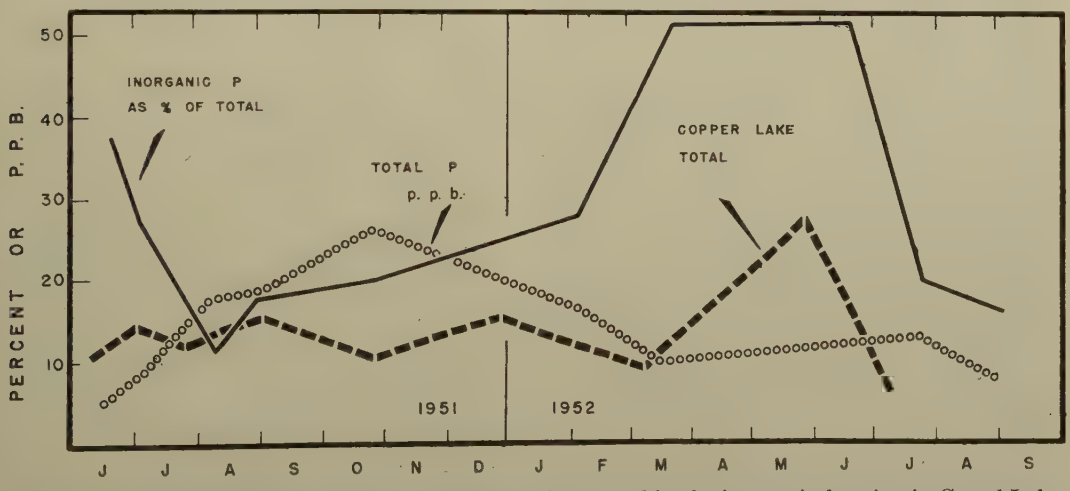


FIG. 5. Variation during the year in total phosphorus and in the inorganic fraction in Grand Lake. Total P for Copper Lake is also shown. The inorganic curve is typical of the three lakes studied, with a winter maximum and a decline in spring and early summer. Variations in total P do not seem to follow any consistent cyclical pattern in the three lakes.

ran through all three lakes, nor were there conspicuous differences related to summer stratification. Variations appear to be due to rain and wind rather than to any productivity cycle.

The variations in phosphorus are more enlightening (Fig. 5). Taking total P first, there was a late summer maximum in Grand in October 1951, but a similar maximum did not appear to be developing in 1952. In Copper lake there is one high spring point in 1952. Fluctuations in the Punchbowl were random, and are not shown on the graph. It is concluded that no consistent seasonal variation in total P takes place in these lakes.

As regards per cent inorganic P the three lakes agree, and the graph for Grand is typical (solid line Fig. 5). There is a decline in early summer (both summers) followed by a rise to a winter maximum. Our interpretation is as follows, being supported by experiments given in paper IV of this series: Bacteria in the absence of plants will equilibrate phosphorus so that about one-half in solution is inorganic. This is the winter condition shown in Grand Lake, Punchbowl being somewhat higher at 65 per cent, Copper lower at 30 per cent. Plants, which start up in the spring, remove inorganic phosphorus quite rapidly to a minimum, which presumably limits plant growth. The spring decline in inorganic P occurs in the sea (Harvey 1945) as well as in lakes (Pearsall 1930). The plants cannot take up organic phosphorus effectively. Later in the summer the plants decline and the inorganic P begins to rise again. Whether, given more observations, Figure 5 could be expected to show a variation in total P corresponding to that of the inorganic fraction is not known. The plants may themselves be liberating organic P, and there may be a seasonal variation in the bacterial population.

A word may be added about the effect on phosphorus of stratification in the Punchbowl, the only one of the three lakes with a strong oxygen deficit in the depths. Unlike the other two, the upper and lower strata here behaved differently, because of inorganic P produced in the depths, both in summer and winter. During full circulation there was equalization. As already noted, the phosphorus from the depths is not sufficient to increase the surface value appreciably when the lake is mixed.

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# Lake Water and Sediment

## II. Oxidation-Reduction Relations at The Mud-Water Interface[1]

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ABSTRACT

Redox potentials of mud cores from seven lakes, including acid bog, unproductive, and productive types, were measured with Mortimer's multiple electrode. A break existed below the surface, but variation in measurement was too great to characterize its depth within ±30–50%. Accuracy of potential measurement is limited by lack of poise, so that the scatter of units of the multiple electrode increases as a standard solution or a natural mud is diluted with distilled water. With the muds studied the scatter was ±50 mv. In poorly poised systems the area of platinum is also important, so that potentials of 0.01 to 0.42 volts were obtained on the same sample with electrodes of different sizes. The presence of $H_2S$ causes a voltage drop, *e.g.*, 20-min. bubbling of a reduced solution with $H_2S$ caused the voltage to fall from 0.63 to 0.17 v. Production of $H_2S$ in nature is abolished by $O_2$. As a further difficulty the sediments of some lakes are able to deposit a sulphide plating on submerged platinum. Evidence is presented that the real oxidized layer is one mm or less thick, and that the reported break in the electrode curve at about one cm is caused by factors other than oxidation of iron salts, *e.g.*, turbulent stirring of the sediment by wind-induced currents, and presence of sulphide.

Several workers have stressed the importance of oxidation-reduction relationships in lake economy. Einsele (1938) related the equilibrium of ferrous to ferric iron to the concentration of phosphorus in the water. Ohle (1938) has made the same comparison for manganese and phosphorus, while Pearsall and Mortimer (1939) have studied the general effects of redox reactions on the commoner ions in solution in lakes.

Einsele's work would seem to place ferric iron at the center of an insoluble complex, which holds nutrients out of solution. During summer when the depths of a stratified lake are depleted of oxygen, the iron is reduced to the ferrous state and, together with nutrients, comes into solution (unless precipitated as FeS). At the autumn overturn the iron becomes ferric again and goes out of solution as $FePO_4$ and $Fe(OH)_3$ in that order. The ferric hydroxide has the ability to adsorb phosphate onto its surface when it is in the colloidal form in the water. The equilibrium between the gel and adsorbed phosphate has been studied by Einsele and by Ohle (1953) and is discussed in another paper of this series.

Mortimer (1942) in an extensive study of the lakes of the English Lake District uncovered many important relations between oxidation and reduction of the mud and the presence of certain ions in solution in the water. He says (p. 306): "The reduction of ferric iron results in the destruction of insoluble ferric complexes previously existing in the mud surface, and in the liberation to the water of bases, including ammonia, adsorbed on these complexes, as well as ferrous iron and other reducing material." Thus when the mud surface is reduced through oxygen depletion in the water, an increase in ammonia, phosphorus, and iron, as well as in alkalinity and conductivity, is observed in the bottom water. Where the biotic activity is great enough under winter ice cover, the phenomena accompanying oxygen lack occur then as well. In a lake whose depths do not suffer summer oxygen depletion, the chemical changes are not observed.

In addition to the reactions resulting from

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oxygen depletion in the depths, the rate of depletion itself may furnish an index of lake productivity (Strøm 1931), as may the consequent $CO_2$ production (Einsele 1938, Ohle 1952). Hutchinson (1938) showed that, in a series of geographically separated and morphologically different clear-water lakes, the hypolimnetic deficit of Strøm is proportional to the standing crop of plankton. See also Hayes and MacAulay (1959) in the present series of papers.

The lower strata of mud are at all times reduced, but the layer at the interface may be oxidized by the water above. Mortimer (1942), developing a discussion by Grote, proposed that the thickness of the oxidized layer of mud during water circulation, *e.g.*, after autumn overturn, could be related to the productivity of a lake. It might be supposed that different lakes have different qualities of mud, as have different kinds of farming land. They might support different numbers of active microorganisms, hence remove oxygen at different rates. If the oxygen concentration at the interface were constant, say at atmospheric tension, the depth of its penetration would be in inverse relation to the oxygen-absorbing power of the mud. One might think of the oxygen molecules like football players trying to make a run through an opposing team of bacteria. The stronger the bacterial defense the sooner the oxygen players will be brought down. Mortimer lowered a multiple electrode into the undisturbed mud of five lakes collected in winter, and recorded the depth at which the potential changed sharply. This was compared with another

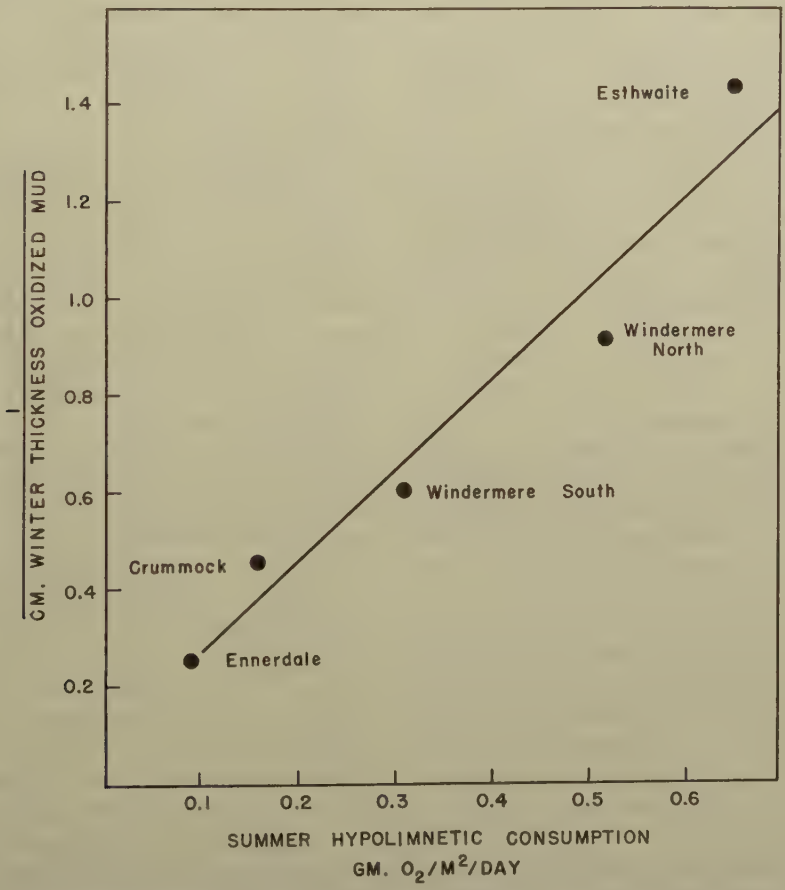


FIG. 1. Data of Mortimer on English Lake District lakes. Reciprocal of the winter thickness of oxidized mud in cm plotted against the summer hypolimnetic deficit.

index of productivity, the rate of generation of the summer hypolimnetic deficit, with results as shown in Figure 1. Agreement between the two measurements was good, suggesting a possibly useful method in regional limnology. If the relationship shown in Figure 1 were widely applicable, the mud potential measurement would be a most valuable index of lake fertility. It would present considerable advantages over field hypolimnetic oxygen studies, which require several visits to a lake and are in any case applicable only to certain types.

The work to be reported in this paper began in 1951 as a naive attempt to use Mortimer's method for the purpose of setting a numerical value on the productivity of lakes in the Maritime Provinces of Canada. In measuring the thickness of the oxidized layer however, various technical difficulties intervened. A minor one was that muds from some regions do not exhibit, under any conditions, the 0.2-volt ferrous-ferric break which Mortimer used as an end point. This and other limitations will be discussed below and an attempt made to evaluate the method. Some attention will also be given to the cause and meaning of the change in potential reading with depth, and a query raised as to whether the oxidized layer is as thick as these measurements suggest.

## METHODS

The theory of potential differences set up in ionizable systems is given by Hewitt (1950), and by ZoBell (1946) who also deals with the application of the method to marine sediments. Bacteria appear to be the principal dynamic agents that affect the redox conditions of muds and soils.

Undisturbed mud cores with lake water over them were taken by the Jenkin apparatus as described by Mortimer, the center of which is a glass tube of diameter about 6 cm and length 60 cm. The cores were brought to the laboratory in a portable refrigerator, chilled by proximity to solid $CO_2$, and were stored in a refrigeration room at 4°C. Obviously an oxidized surface layer of mud would only be expected when there was oxygen in the water over the mud. Except in unstratified lakes, fully oxygenated water would occur only at spring and autumn turnover. Mortimer measured "winter thickness of the oxidized layer" when the lake was in full circulation. In the present work the samples were taken in summer and air was bubbled through the water for 24 hours before measurements were made.

Pearsall and Mortimer (1939) observed that ferrous iron appeared in the waters of Blelham Tarn, and also in soils and muds, only if the potential fell below 0.23 volts, which in Blelham Tarn corresponded to an oxygen concentration of 0.5 ppm. They took a potential of 0.20 volts, corrected to pH 7.0, to represent the break between oxidation and reduction. This was in practice the flat part of a depth-voltage curve. Since in the present work the 0.20 voltage was not always reached, the point of inflection was used, regardless of voltage. An ideal curve looks like a temperature-depth curve in a stratified lake, and our chosen break would correspond to the center of the thermocline in such a plot.

A multiple platinum electrode was built as described by Mortimer, and illustrated in his Figures 16 and 24, being twelve electrodes bound together like steps of a spiral staircase. In the text below they are referred to by number with reference to their distance in mm above or below the mud surface, as initially or ordinarily used, *viz.* 50, 10, 1, −1, −2, −3, −5, −7, −10, −13, −16, and −19. Where the context below so indicates, the numbers should be read as identifications of electrodes, not as depths. Because of the spiral arrangement each electrode cut the sediment at a new, undisturbed spot. Each electrode measured 2 x 10 mm, and was sealed with a short length of platinum wire into a glass tube extending above the water. To make readings the wire from the potentiometer was clipped onto the different electrode leads in succession.

The system was initially lowered into the sediment until the +1 electrode just touched the surface, whereupon the middle of each electrode was called its depth. Later the whole system might be pushed farther down. Raising and lowering was accomplished with

a microscope rack and pinion for smooth operation. Following Mortimer, two hours were allowed to elapse before readings were taken. Most of the drift, however, occurred in the first ten minutes.

In some tests a single platinum electrode in a form of one $cm^2$ of foil was used; this is referred to as the "large" electrode, being five times the area of each unit of the multiple electrode. A platinum wire one cm long and 1.15 mm in diameter was also used, being called the "small" electrode.

Electrodes were standardized before use, latterly in a solution recommended by ZoBell—a mixture of M/300 $K_3Fe(CN)_6$ and M/300 $K_4Fe(CN)_6$ in M/10 KCl. The $E_h$ value is 0.43 volts at 25°C. Before use in sediment the electrodes were washed in dilute nitric acid and well rinsed.

The pH of the sediment was taken, and potential readings corrected to pH 7 as done by Mortimer. Thus our $E_7$ is directly comparable to that of Mortimer.

## POTENTIALS OF CORES

Over several summers twenty series of potentials were measured on mud-water cores from seven lakes in imitation of Mortimer. One from each lake, not necessarily the best, is shown in Figure 2. The lakes will be briefly mentioned, being characterized in the opening paper of this series (Hayes and Anthony 1958).

Southport Pond, P.E.I., is a productive, artificial, former mill pond in agricultural land. Practically all mud readings appear to be less than those of the water, and it is difficult to perceive an inflection point in the curve unless it is assumed that the inflection is too close to the surface to be measured by the electrode system, say at 1 mm or so.

The Punchbowl is an extreme acid bog type surrounded by *Sphagnum*. The inflection might be placed between 0.5 and 1 cm.

Copper Lake lies in poor agricultural country. The break, at a guess, would lie at a depth not greater than 0.5 cm.

Grand Lake has poor farms at one end and barren granite country at the other. It is judged unproductive. It presents the best approach to an ideal curve of potential with a break at 3.3 ± 0.5 cm.

Lily Lake is in marginal farm area. The curve scarcely reaches Mortimer's 0.2-volt ferrous-ferric line, and the slight break might be centered at 1.0 to 1.5 cm.

Bluff Lake is very primitive and very unproductive, in a granite area. There is little fall in potential (never to 0.2 volts), and any break is ill-characterized, lying perhaps between 1.0 and 2.3 cm.

Black Brook Lake too shows little drop in potential, and its scattered points might inflect anywhere between 1 and 3 cm. This lake too is in marginal farming country.

Surveying the group it appears that the depth of the break in potential can generally be identified to within ±30 to 50%. The most productive (Southport) has the thinnest layer above the break, if any meaning at all is to be drawn from the points. The Punchbowl may be lower than most of those to follow. On other measurements in this laboratory, such as bacteria in the sediment and oxygen consumption above a mud core, the above two are about alike. The rest of the group of lakes are, in our other estimates, placed in an order not related to that suggested by mud potentials. Among the several other lines of investigation of productivity which are in progress here, there is a degree of harmony emerging, which however does not include the potentials, except to a limited extent for the first two lakes mentioned.

The considerable scatter in Figure 2 and the variability in the shape of the plot from lake to lake, led to an examination of the technique employed and to an inquiry as to whether the curves might have a more complex and variable meaning than was suggested in the introduction.

## LIMITATIONS OF POTENTIAL MEASUREMENTS

In using his compound electrode, Mortimer found that the mud potential readings fell rapidly to a "fairly steady state after 1–2 hr. A slow negative drift was observed over a period of days." He cleaned in dichromate-sulphuric, a high potential mixture. When the multiple electrode was immersed in a well-mixed sample of reduced mud, usually his readings on each unit agreed to within ±10 mv, although anomalous behavior of

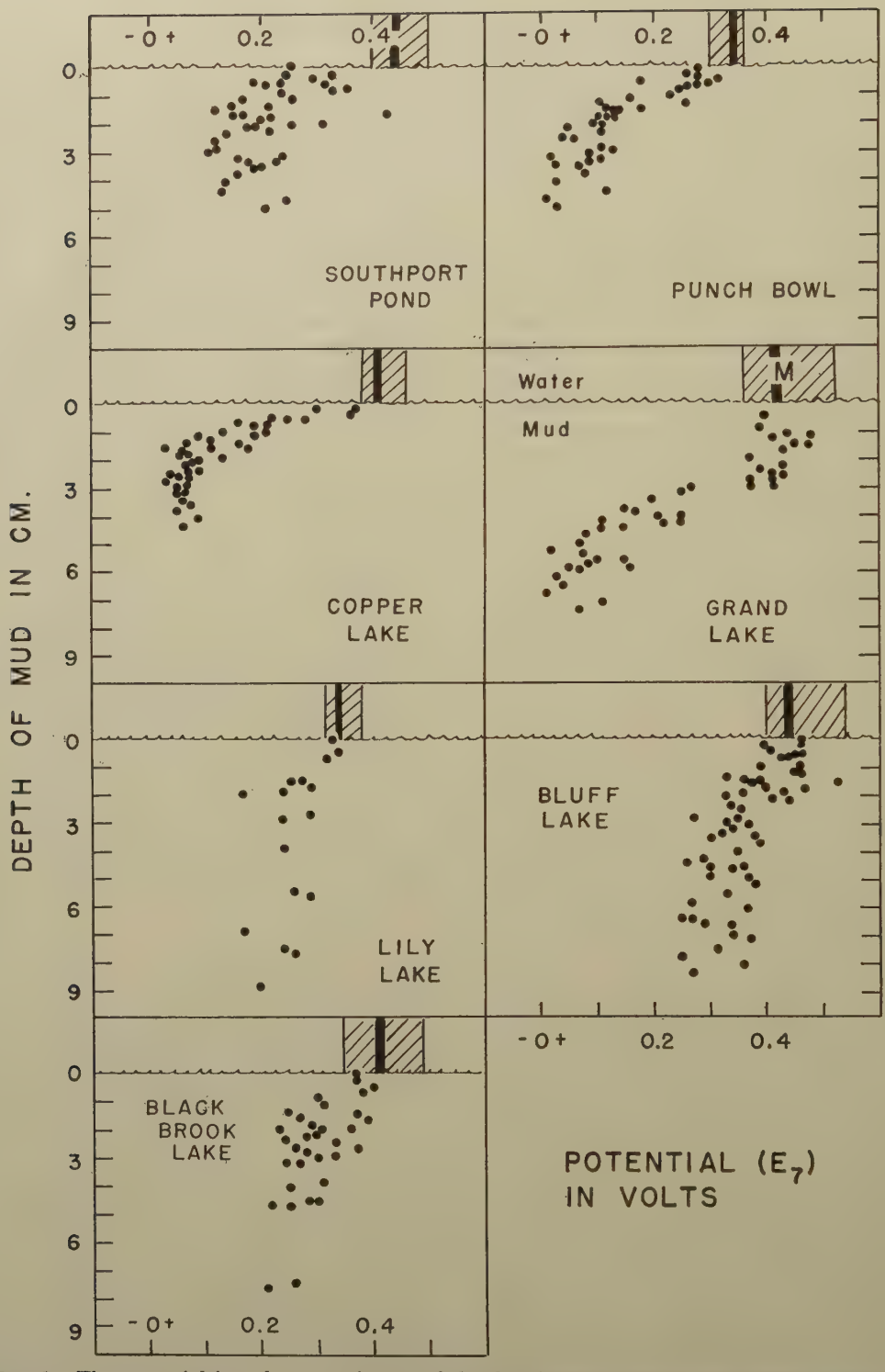


FIG. 2. The potential in volts at various mud depths of seven lakes. These were typical of the twenty tests made. Collections were made in summer, and the multiple electrode was lowered into the Jenkin core after two hours' bubbling of the water with air. Except for the Punchbowl, which suffered summer oxygen depletion in the depths, there was oxygen present over the mud when collection was made. The several measurements of water potential are averaged as the central line, and the range is shown as a shaded band. The central line is identified by the letter *M* on the Grand Lake chart.

single electrodes occasionally occurred. We did not attain such accuracy; ±50 mv would be a modest scatter in mud. With us, and presumably with Mortimer, all electrodes were absolutely on the mark when tested in standard solutions. The trouble arises when lake samples are used.

A test showed that one source of variation was lack of poise in the muds. This is equivalent to lack of buffering capacity in pH tests which, as is well-known, makes measurements difficult. Dilution of a standard or a lake sample by distilled water will lower the poise. A measure of dilution is given by the electrical conductivity of the solution. Figure 3 shows how the errors of individual electrode measurements increase with dilution of the ferriferrocyanide standard. Dilutions of well-mixed mud from Silver Lake, a moderately acid bog type, which are less regular in behaviour, are included for comparison. The lakes studied by Mortimer had about twice the conductivity of those reported on here.

As ZoBell has pointed out, the area of platinum in electrodes becomes critical in poorly poised systems. Also any small adsorption of poising substances on the platinum becomes noticeable. This was shown in a test where the effect was observed of cleaning the large electrode in dilute nitric acid (high potential) or dilute NaOH (low potential) before use. Readings following thorough washing and subsequent immersion in 1% standard, are shown in Figure 4. There was a marked drift which had not yet reached equilibrium in 15 minutes. This is because the diluted solution, by reason of loss of poise and conductivity, is approaching the condition of distilled

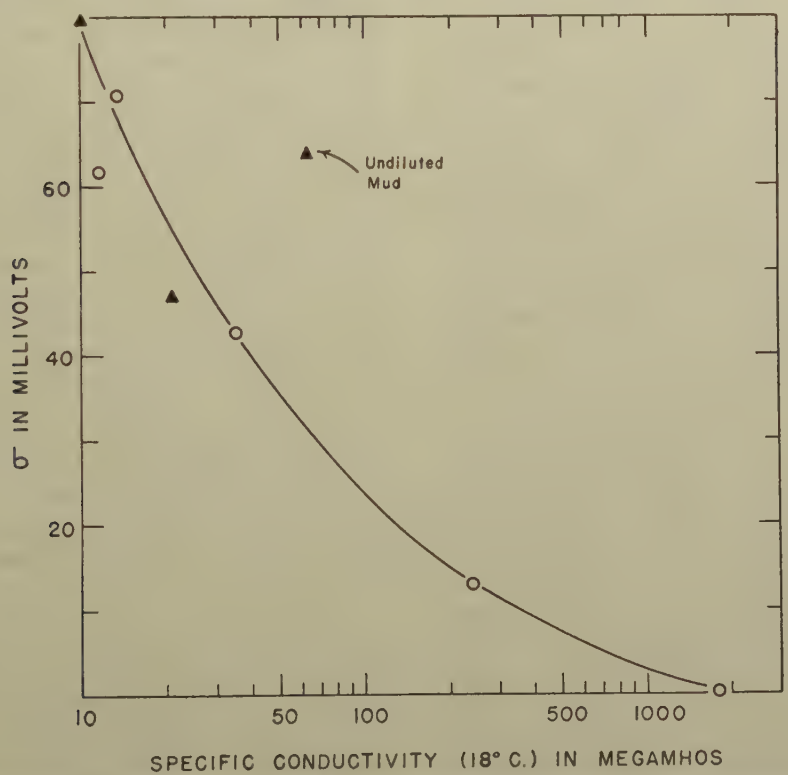


FIG. 3. The effect on errors in potential readings, caused by dilution of standard solution (circles) and of Silver Lake mud (triangles). The labelled triangle is full-strength mud, while the other two are diluted with distilled water. The ordinate represents the standard deviation of the series of 12 units of the multiple electrode, expressed as millivolts. Any one electrode of the group will have a 2:1 chance of deviating not more than the value shown, above or below the purported correct value (which is, in the example, the mean of the 12).

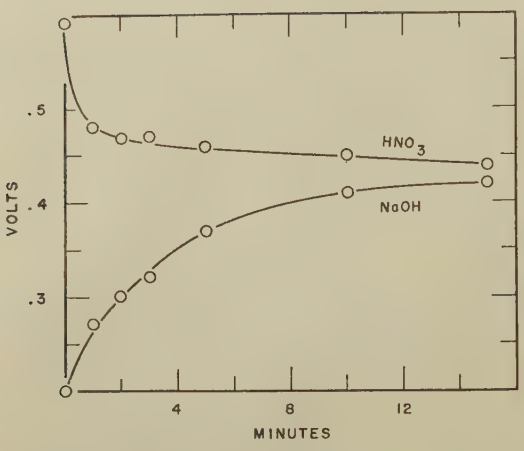


FIG. 4. Effect of the method of cleaning the large platinum electrode on the potential drift in 1% standard solution, whose conductivity was measured as 165 megamhos. After treatment with dilute acid or alkali the electrode was rinsed very thoroughly in distilled water. At zero time the electrode was lowered into the test solution.

water. When the multiple electrodes of small area were similarly tested, the scatter was so greatly increased that no trend towards adjustment was apparent on a graph.

To show the effect of area of platinum on the readings, reduced Black Brook mud was well stirred and tested with three units. Results are given in Table 1. It is perplexing to decide which is the true potential. We presume that the large electrode is reading correctly, or more nearly correctly. This is because it does not show a fluctuation in dilute standard comparable to that described for the multiple set (Fig. 3).

A source of error likely to be met in nature is that hydrogen sulphide has a direct effect on potential. For example, the potential of a 0.1 N sulphuric acid solution was determined to be 0.63 volts with the large electrode. After bubbling with $H_2S$ for 20 minutes, the voltage fell to 0.17. The change in potential is about equivalent to the greatest difference found in most lakes between supposed oxidized and reduced muds. Experiments of Wheatland (1955) show that a small amount of oxygen will abolish $H_2S$. This worker bubbled nitrogen ($O_2$ free) through water over mud from a polluted marine estuary and collected $H_2S$ from the issuing gas. Addition of 1% $O_2$ to

TABLE 1. *Effect of area of platinum on apparent potential*

Readings on mixed Black Brook Lake mud after one hour immersion

| Unit | Area mm² | Potential volts |
|---|---|---|
| Small electrode | 36 | 0.42 |
| Multiple electrode mean (range 0.18–0.49 v) | 46 | 0.31 |
| Large electrode | 200 | 0.01 |

the nitrogen had little effect, but 2% or 3% $O_2$ stopped the production of $H_2S$. Oxygen above 2% tension and $H_2S$ cannot exist together. The latter is removed exponentially with a half-life of about one hour. That $H_2S$ effects operate in nature is made probable by the notes to follow on the individual behavior patterns of two lakes.

Grand Lake mud below the level of its potential break (see Fig. 2) will deposit an amber colored plating on electrodes left in it. In this mud, uniquely, there is also a color change at the level of the break. The units of the multiple electrode which were plated drifted down overnight by an average of 0.36 volts from their 2-hour regular reading the day before; the superficial units, not plated, drifted down only 0.15 volts. The amber plating required several rinsings in conc. chromic acid for removal. General chemical considerations suggest that the plate was a sulphide (Mellor 1947). For one thing platinum carbonates have never been found, while the nitrate is formed in the laboratory only with difficulty, and the sulphate only by boiling. On the other hand platinum is readily acted on by $H_2S$ or ammonium sulphide. Upon degassing after $H_2S$ treatment, hydrogen is evolved, leaving the sulphur as a deposit.

It was found that copper wires became similarly plated below the 3-cm level. Upon chemical testing the plate was found to be soluble in $HNO_3$, KCN, and warm HCl. It was insoluble in $NH_4Cl$, $NH_4OH$, water, and organic solvents. When the KCN solution containing the unknown was acidified and heated in a test tube with lead acetate paper over the mouth, the paper turned black. These reactions suggest a sulphide, but not iron sulphide, which is in-

soluble in KCN; presumably it was copper sulphide.

Five other lakes tested failed to give a plating reaction.

Another peculiarity, provisionally attributed to $H_2S$, was demonstrated in Punchbowl mud. A sample that had been in the laboratory for several days was noted to have a strong $H_2S$ odor. Its potential was $-0.23$ volts, the lowest observed in this work (large electrode). Some of this mud was put in a large pressure flask and evacuated for one minute while being gently rolled around the walls. Upon replacement with air the potential was 0.21 volts. In a similar evacuation, followed by replacement with nitrogen, the potential was 0.13 volts. During the course of the next half hour it fell again to $-0.14$ volts. It is concluded that one or more volatile substances, including $H_2S$, affect the potential in a manner that is additional to any simple reduction.

Three other lakes tested failed to show the reaction.

Difficulties of the kind just outlined led Wartenburg (1935) after an extended survey of the agricultural field, to conclude that any reported correlations between redox potentials and soil properties are due to special circumstances and particular methods and are not explainable on a basis of true theoretical considerations.

### WHAT DOES THE MULTIPLE ELECTRODE MEASURE?

In some of our muds, *e.g.*, Grand Lake, there is a lighter layer at the surface, whose appearance suggests rust-colored ferric compounds, contrasted with darker or supposed ferrous material below. Attempts were made to produce such a layer in laboratory preparations. When mud is placed in the bottom of a vessel and covered with water, a lighter brown color does soon become observable at the surface, and over the course of a few days it moves down to a depth of about 0.5 cm. Preliminary tests had included air bubbling, so that the surface was at first taken to be oxidized. However the layer is seen also with nitrogen bubbling or under stagnant water. The cause is unknown. The same lighter layer is observed in marine mud upon standing (Wheatland 1955).

Tutin (1955) offers evidence that the surface sediment of Lake Windermere is stirred by the water over it. Diatom and algal cells were observed to sink through the water and disappear into the mud during the summer, following their spring maximum. After the first autumn gale there was an enormous increase in the numbers of dead cells in the surface waters; these cells then slowly sank again. Thus a break in potential might be taken to mark, not "winter thickness of the oxidized layer" but the depth to which turbulence had stirred up the sediment. From lake to lake it might depend on the shape of the basin in relation to wind effects. For example, an acid bog lake like our Punchbowl would be minimally stirred, having a *Sphagnum* mat encroaching from the sides to give the basin a thistle-tube shape.

According to Vallentyne (1955), "Experiments show that oxidized mud settles completely from suspension more quickly than reduced mud. This is apparently caused by an increased sediment particle size, and perhaps an increased density also, accompanying oxidation."

The production of sulphide in the mud represents a second means of affecting potentials. $H_2S$ might be expected to diffuse out into the water to an equilibrium condition. In an unproductive lake there would be less sulphide formed, hence a thicker surface layer sufficiently free from it so that potentials would not be depressed. In more productive lakes the sulphide effect on potentials would extend closer to the interface. Thus the so-called "oxidized layer" would be in reality a low $H_2S$ layer. Within a geologically similar group of lakes the thickness of the low sulphide layer might be inversely related to productivity.

Combining these effects there might be, after the autumn turnover, an oxidized surface layer which was stirred up and redeposited by turbulence, and which was deficient in $H_2S$. Below it would lie the permanent deposit, reduced and containing $H_2S$. A marked break in potential would be expected between the layers. Its position

would not, however, be an index of productivity. Or would it?

Is it possible that an unproductive lake can have its sediment stirred more easily, hence more deeply, than a productive one? Figure 4 of the first paper of this series (Hayes and Anthony 1958), shows that organic content of the sediment is related directly to alkalinity and to other qualities of increasing productivity, such as Ca and conductivity. Would organic sediment flocculate more than mineralized deposits, hence settle into a thicker layer? In other words, does productive sediment tend to pack better as it falls?

In the light of the doubts and difficulties which have been brought forward in this section, the relation which Mortimer observed between the thickness of the higher potential layer in winter and the rate of oxygen uptake in summer is most remarkable and deserving of further investigation.

### THICKNESS OF THE OXIDIZED LAYER

We find it plausible to suppose that the observed potential curves are related to phenomena more complex than oxidation-reduction. In unstirred mud it is probable that the oxidized layer is one or two orders of magnitude thinner than tests with the multiple electrode would indicate, in fact too thin to be measured by this apparatus. Some evidence of varying weight may be brought forward in support of this opinion.

A depression in the mud was often noted around the multiple electrode, suggesting that the units were carrying down the surface and compressing the lower part. Experiments were tried on lake mud of which a portion was aerated and a portion left reduced. The system was made into two layers in imitation of nature and the potential curve determined. There was some indication, not conclusive, that the redox layer may be pushed down by the electrode, in some muds, by a few mm. Interpretation is made difficult by the change in colloidal texture of the mud caused by preparatory mixing.

A chance field observation showed that when a rusty stovepipe is pushed into sediment at lake bottom, the rust is removed overnight to the level of the interface.[2] This suggested a simple method to indicate the depth of oxygen penetration, and led to tests in which iron and copper wires were placed vertically in mud-water cores. On all lakes results were consistent. Rust was removed from wires not only in deeper sediment, but up to the interface, while the part of the wire in water became more rusty. The water was kept aerated. Rust was removed even in the lighter-colored superficial 3 cm of Grand Lake mud. A cleaned iron wire remained so to the interface even after a month's submersion. Iron wires suspended horizontally from non-conductors gave the same results. Copper wires, vertically suspended, became tarnished in the water but remained clean in the mud even when left for a month. Grand Lake provided an extra feature in that the clear zone extended down for 3 cm only, below which a black deposit formed. The deposit that formed after a month of immersion was scraped off and tested chemically; it proved to be a sulphide, presumably copper sulphide. It was not iron sulphide.

In an experiment in which radiophosphorus was added to water over a core it was found that about half the activity had left the water within a fortnight. At this time a dental X-ray film was inserted vertically into the mud for 48 hours, then developed. This radio-autograph showed the activity concentrated in the top mm or less of mud. For a more accurate estimate of activity as related to depth, samples similarly treated were frozen and sliced on a microtome. The results given in Hayes (1955, p. 113) show that almost all the activity in the mud is concentrated in a layer at the surface estimated as less than 0.5 mm thick. Microscopic examination of this layer showed it to consist of organic debris containing a few diatoms and other green unicellular organisms and huge numbers of bacteria. The extreme concentration in a

[2] A reader of the MS suggested that the question of who pushed a rusty stovepipe into a lake bottom, and why, had a quality of mystery and should be explained. It was Dr. D. A. Livingstone, who lost the casing of his deep piston sampler and made a field substitution of stovepipe.

surface layer is not observed in artificial mud cores, hence may be due to some natural event such as a phytoplankton fall-out.

Vallentyne (1957) made extracts of chlorophyll degradation products in lake sediment cores. It is well known that pollen grains are present in the deeper parts of such cores, which are considered to be over 10,000 years old. Vallentyne found in addition to chlorophyll products "surprisingly high amounts of free hexose and pentose sugars, as well as beta-carotene and myxoxanthin." If such substances were oxidized for a long period it is unlikely that they would be preserved. Now the rate of sedimentation varies from lake to lake, but it might be taken that the thickness to the potential break represents several years' deposit. If the depth to the potential break were the depth of oxygen penetration, it would imply that simple sugars were subject to oxidizing conditions in the presence of bacteria for several years, or at least several winters, and survived, a conclusion which is difficult to accept.

The "several years" mentioned in the foregoing paragraph works out as four years from the following data. Tutin (1955) gives the annual deposit of Lake Windermere as 2.5 mm, while Thomas (1955, p. 465) gives for Swiss lakes, values of 1.8, 5.1, 4.4, 3.8, and 7.4 mm, with a mean of 4.2 mm. For comparison, the mean depth of potential break for Mortimer's five lakes is 19 and for our six lakes 17 mm (omitting Southport). Dividing 18 by 4.2 gives 4 years as the exposure time to oxygen of a given sediment particle, *i.e.*, if the potential break were to be regarded as an indication of oxygen penetration.

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# Lake Water and Sediment

## III. The Effect of pH on the Partition of Inorganic Phosphate Between Water and Oxidized Mud or Its Ash[1]

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ABSTRACT

Dried and reconstituted mud from pairs of primitive, medium, productive, and acid bog lakes was shaken to phosphorus equilibrium with water. Minimal P was released at pH 5.5–6.5, and ranged from scarcely above the level of chemical detection up to 0.2 ppm in productive lakes. Further acidity caused a slight increase of P in the water, up to 0.3 ppm, and alkalinity a larger increase, up to 0.5 ppm. At all pH levels the quantity released increased in the order of lake types stated above. The pH versus P curve for whole mud was shallow or saucer-shaped; ashed mud gave a similar but deeper or cup-shaped curve. Thus a productive lake ash at pH 4 released 1.0 ppm and at pH 8, 1.2 ppm. When 1 ppm of P was added to the water prior to the shaking, the lake type reacted differently. Acid bog and productive lake muds left the added P in the water, while unproductive lake muds removed most of it under acid conditions but not at pH 7 or more. The adsorption behavior of ash is similar to that of Bentonite, Fuller's earth, or ferric hydroxide gel.

The application of phosphate to soils with a view to improving crop growth goes back to the early 1800's, when ground bone came into use as a fertilizer. The stimulating effect was at first slow until in 1840 Liebig suggested that a more soluble form of phosphate be made by treating bone meal, and later mineral deposits of $Ca_3(PO_4)_2$, with sulphuric acid, as has since become general practice. In 1877 Panknin suggested that if sulphur were mixed with tri-calcium phosphate before use, the Liebig effect would take place in the soil due to the production (as was later found) of sulphuric acid by bacteria. The quantitative relations of the sulphur reaction as it occurs under bacterial influence were worked out by Lipman & McLean (1916), who also showed that the reaction goes forward more effectively in good soil than in Sassafras loam or sand.

Several agricultural workers have added super-phosphate $Ca(H_2PO_4)_2$ and calcium to soils together, and found that the P becomes bound again. The mechanism may be re-formation of apatite or adsorption of the P on calcium carbonate crystals. References are given by Zicker *et al.* (1956), who demonstrated the same process in laboratory tests with bog lake sediments. Addition of acid to their samples could release the bound P once more.

The incompatibility of Ca and P in soils does not apparently carry over to the aquatic situation; according to Wunder (1949) the effect may be disregarded in water. Wunder stresses that superphosphate is of little value in carp ponds without previous liming.

In tracer studies outlined by Parker (1950), either superphosphate or rock phosphate labelled with $P^{32}$ was added to soil at the rate of 350 lbs $P_2O_5$ per acre. With superphosphate there was a higher crop yield (of vetch); the plants contained a higher percentage of phosphorus, and the percentage derived from the fertilizer was greater. There was, however, an improvement in rock phosphorus uptake caused by acid so that its deficiency was least at the

[1] The writers are indebted to the Nova Scotia Research Foundation and the National Research Council of Canada for financial aid.

lowest pH tried, as the following comparison of relative effectiveness shows. The figures are proportional to the mass of phosphorus from fertilizer which was removed from the soil and incorporated into the plant body.

| soil pH | rock phosphate | superphosphate |
|---|---|---|
| 4.9 | 42 | 90 |
| 5.5 | 26 | 93 |
| 5.8 | 15 | 93 |

The foregoing sketch shows how intimately the behavior of phosphate is bound up with the acid level of the soil. In a natural mud-water system at equilibrium there is almost no phosphate left in the water. By comparison with agriculture there is relatively little known about the aquatic mechanism, and this prompted the tests reported here on soils from several lakes.

The principles and practice of pond fertilization have recently been extensively dealt with by Mortimer and Hickling (1954).

## METHODS

The mud used in these experiments was collected from the lakes in Table 1 by dredging the bottom to a depth of some 10 cm. It was air dried in thin layers at room temperature and, following standard sampling techniques, was ground finely enough to pass completely through a standard 40-mesh sieve. Uniform samples of a few hundred grams from all of the lakes were prepared in this manner and stored in screw-top bottles. A portion of each such sample was ashed in a furnace at a dull red heat, the loss in weight determined, and the ashed samples were stored in stoppered bottles. Table 1 gives the percentages of ash in the muds. These percentages also represent the amounts of ash in milligrams used in the experiments that follow, *i.e.*, the amounts of ash equivalent to 100 mg dried mud.

The experiments were designed to measure the distribution of phosphate between a solid phase (mud or the equivalent amount of dried mud) and an aqueous phase (water, with or without *added* phosphate, at various pH's). The system, in a stoppered 125 ml Erlenmeyer flask, consisted of 100 mg of the sieved, dried mud (or its ash equivalent) in

TABLE 1. *Summer pH of water and per cent of ash in sediments of lakes*

The ash figure also represents, in mg, the amount taken for a test. As all of the lakes except Montague and Southport are but very slightly buffered, the pH values do not have much meaning.

| | pH of water | % ash in dry sediment |
|---|---|---|
| Punchbowl | 5.2 | 43.0 |
| Silver | 5.2 | 64.7 |
| Montague | 8.3 | 84.2 |
| Southport | 8.9 | 83.8 |
| Copper | 7.3 | 76.8 |
| Lily | 6.4 | 61.5 |
| Grand | 6.4 | 73.3 |
| Bluff | 5.3 | 57.5 |

an eventual volume of 50 ml. However, before making to volume, 0.01N HCl or NaOH was added to the series of mud or ash samples in amounts necessary to give a range in pH values, and in addition in some cases an amount of a standard phosphate solution equivalent to 50 mg P. De-ionized water was then added to give a final volume of 50 ml.

Each flask and its contents was then mechanically shaken for one hour (it was found that equilibration of the two phases was achieved in this time), following which the solid phase was filtered off, and the pH and the phosphate content of the filtrate determined. The pH measurements were made on a portion of the filtrate using a standard glass-electrode pH meter. The phosphate, in a range of 5 to 50 $\mu$g P in a final volume of 50 ml, was determined by the usual reduced phosphomolybdate method, using freshly prepared stannous chloride as the reducing agent (so as to achieve maximum color development) and matched 100 ml test tubes as cuvettes (to take advantage of the 2½ cm light path and the resulting increase in sensitivity). The optical density of the colored solutions was measured at a wave length of 730 m$\mu$ with a Beckmann Model B spectrophotometer.

The limiting factor on measurements of phosphate at the alkaline end of experiments with whole mud was increasing turbidity of the filtrate which eventually raised the blank to an unmanageable level. The phosphate in some samples could be determined with satisfactory accuracy above pH 9,

others scarcely to pH 8. Turbidity blanks could be obtained either at 730 mμ, the wave length of final measurement before reagents to develop the color were added, or at 550 mμ after development of color. The wave length of the blue color is approximately 550 mμ, so that any turbidity would show maximally there. Knowing the difference in optical density of standard phosphate at the two wave lengths (550 mμ turned out to be about 44 per cent of 730 mμ), and assuming that turbidity will show equally at both wave lengths, the necessary correction can be made.

## EXPERIMENTS

The samples used came from eight lakes, descriptions of which are given by Hayes and Anthony (1958). The lakes fall conveniently into pairs, being judged to be of four types, namely acid bog, productive, moderate or medium productivity (draining marginal farm land), and unproductive (draining granite-quartzite). In the illustrations the members of each pair are set up side by side or are averaged.

In Figure 1 are shown the results of shaking mud or equivalent ash with distilled water. At the start there was no phosphorus in the water, and if no release had taken place all curves would be horizontal lines at zero level; the curves as drawn show how much did come out at equilibrium. Perhaps the most striking feature is the general similarity in behavior of all the lakes, which are quite scattered in location and geological formation. As between mud and ash there is also a common pattern. One might say that an ash curve sits in a mud curve like a cup in a saucer. The reaction of ash to pH is more extreme but of the same kind as that of whole mud. Thus the organic part of the mud appears to act as a moderator of phosphate release at the ends of the pH range. It is evident that minimal quantities of phosphorus are released to the water at pH values just acid to neutrality, generally from 5.5 to 6.5. With ash the water values rise on each side of the minimum, that towards acidity being less conspicuous. With whole mud also the release of phosphorus to water is less noticeable under acid conditions; indeed in a majority of the lakes there is no convincing upswing at all on the acid side. While alkalinity causes a release of phosphorus from whole mud, there is some suggestion of flattening of the curves, as though further increase in pH would not be accompanied by release of much more phosphorus. Figures 2 and 3 show this somewhat more clearly. Hepher (1958) reports that fixation of phosphorus to the mud is increased by the presence of calcium carbonate. It is at about pH 8.4 that carbonate begins to appear, and this might explain the apparently anomalous behavior of phosphorus at higher alkalinities.

The quantity of phosphorus released at the least favorable pH is minimal in the unproductive pair of lakes, at the bottom of Figure 1. It is in fact at the limit of the analytical method and hardly discernible from zero. The pair of moderately productive lakes releases more at pH 5.5, and the productive pair still more. Finally the acid bog pair behave as though they were productive lakes, although they are located beside the unproductive pair in a quartzite-granite area.

Many of the features just mentioned are more clearly shown in Figure 2, in which equilibration between mud and added phosphate is followed. When mud is shaken with water containing 1 ppm of phosphorus, there should be found in the water both the equilibration P as shown in Figure 1, plus any of the added P that remains. What is illustrated in Figure 2 is the latter portion only. To obtain Figure 2 there was subtracted from the total P observed, the value at each pH from Figure 1. In order to save vertical spaces the upper three pairs do not go to their base lines but are top segments only.

If the mud and its ash had not removed any of the added P, all curves in Figure 2 would be horizontal lines at the 1.0 ppm level. This situation is approximated in Montague and Southport mud and ash where virtually nothing happened. Almost the same may be said of the acid bog whole mud, although its ash took up some P in the mid range. Continuing down Figure 2, it

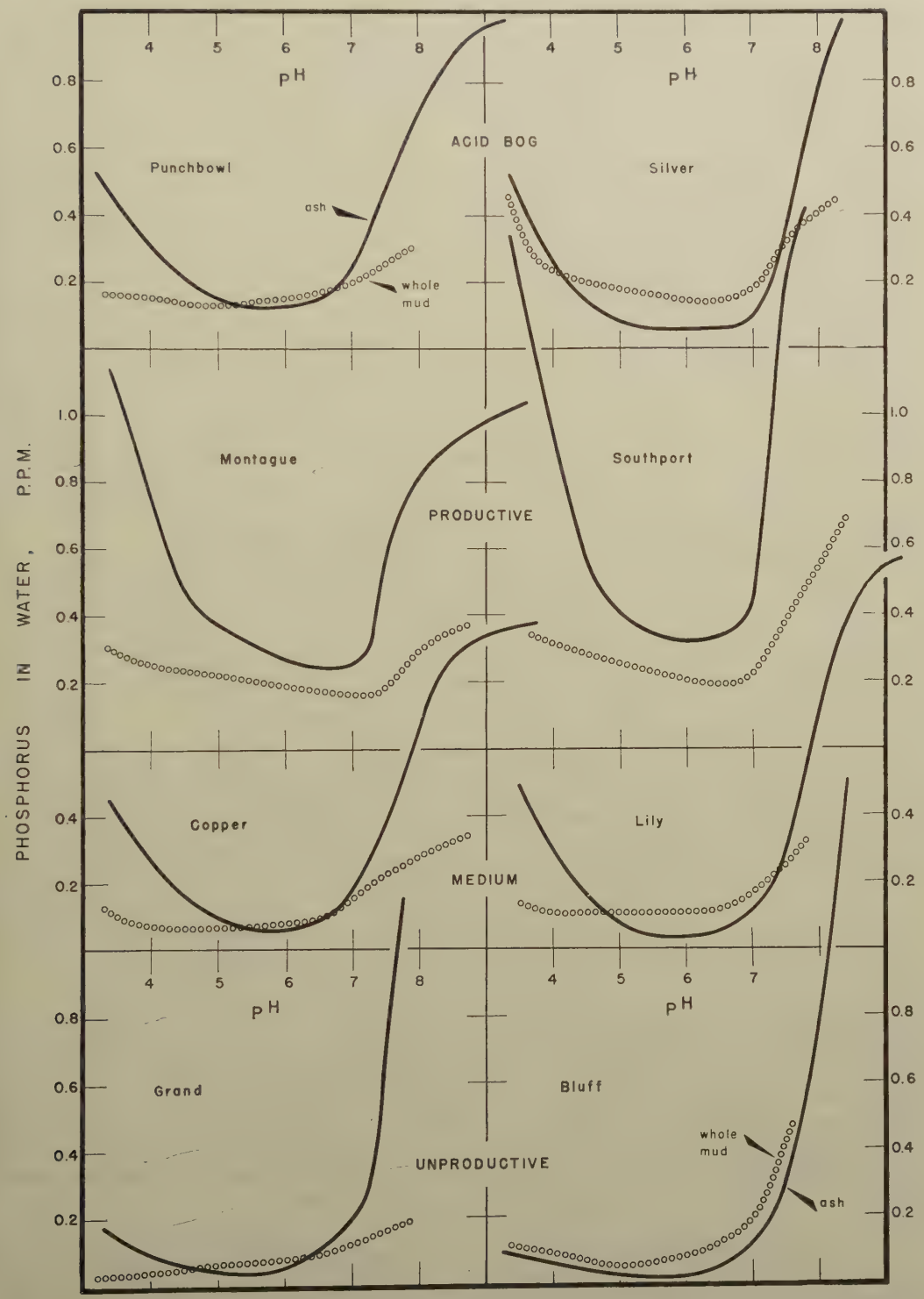


FIG. 1. Relation of pH to inorganic phosphorus which was found in solution after 50 ml of distilled water had been shaken up for one hr with 100 mg of powdered mud, or with the ash from 100 mg mud

is seen that the moderately productive and unproductive pairs of lakes take out successively more P at the trough pH level, and that the ash binds more than whole mud, even to the point of removal of all the added P. These results confirm Figure 1 and suggest that the function of the organic component of the mud is to restrain a fundamentally inorganic response.

Figure 3 sums up the observations in

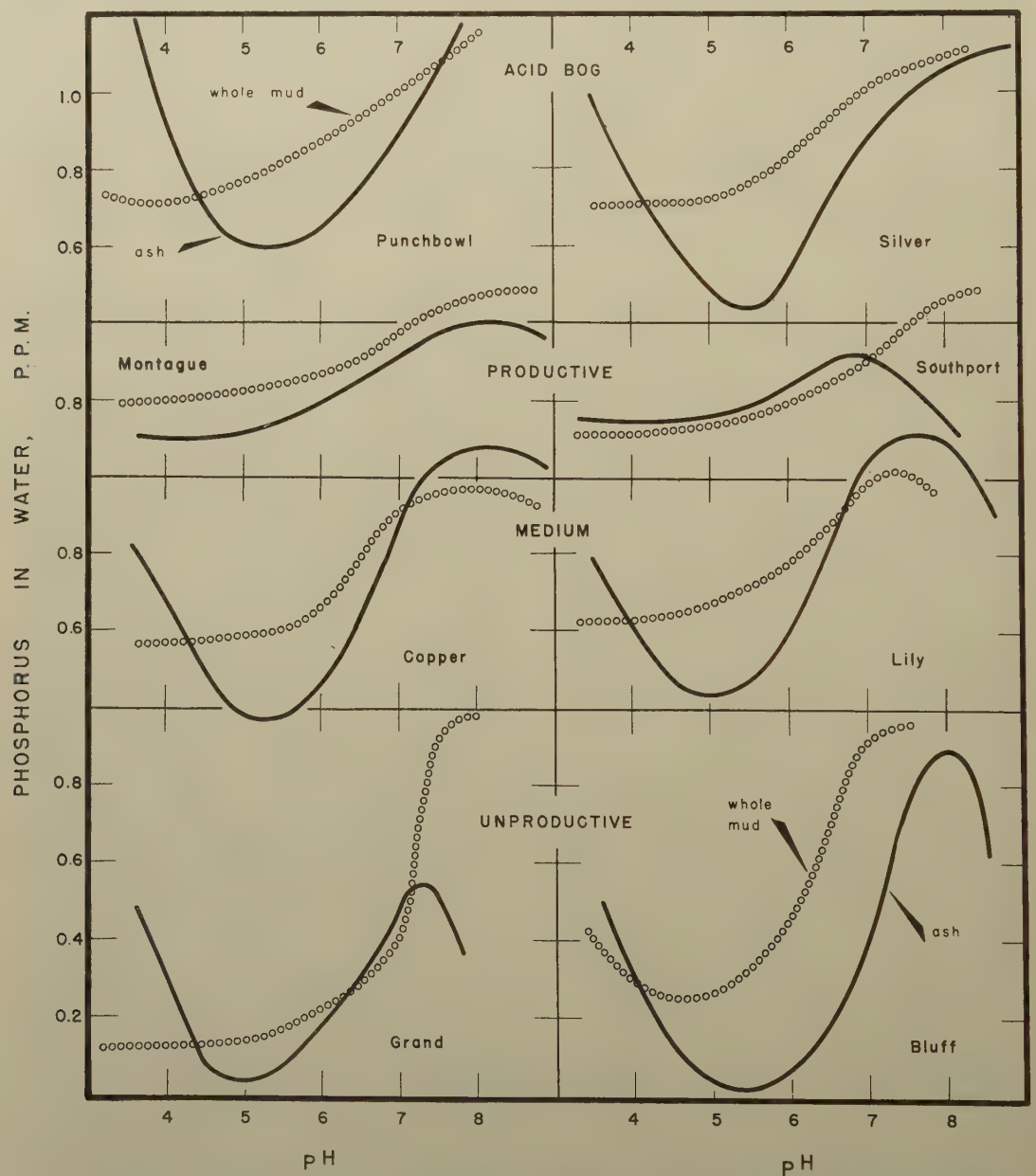


FIG. 2. Effect of pH on ability of mud, or equivalent ash, to remove added inorganic phosphate from water. Experiment as described for Figure 1 except that 50 μg (or 1 ppm) phosphorus was initially present in the water. The curves do not represent the total phosphorus left in the water, but only the part corresponding to the added 50 μg, *i.e.*, they represent total minus Figure 1 values. Thus these curves would not be expected to fall below zero or rise above 1 ppm. That some of them do rise above 1 ppm is a measure of the error involved in subtracting one curve from another.

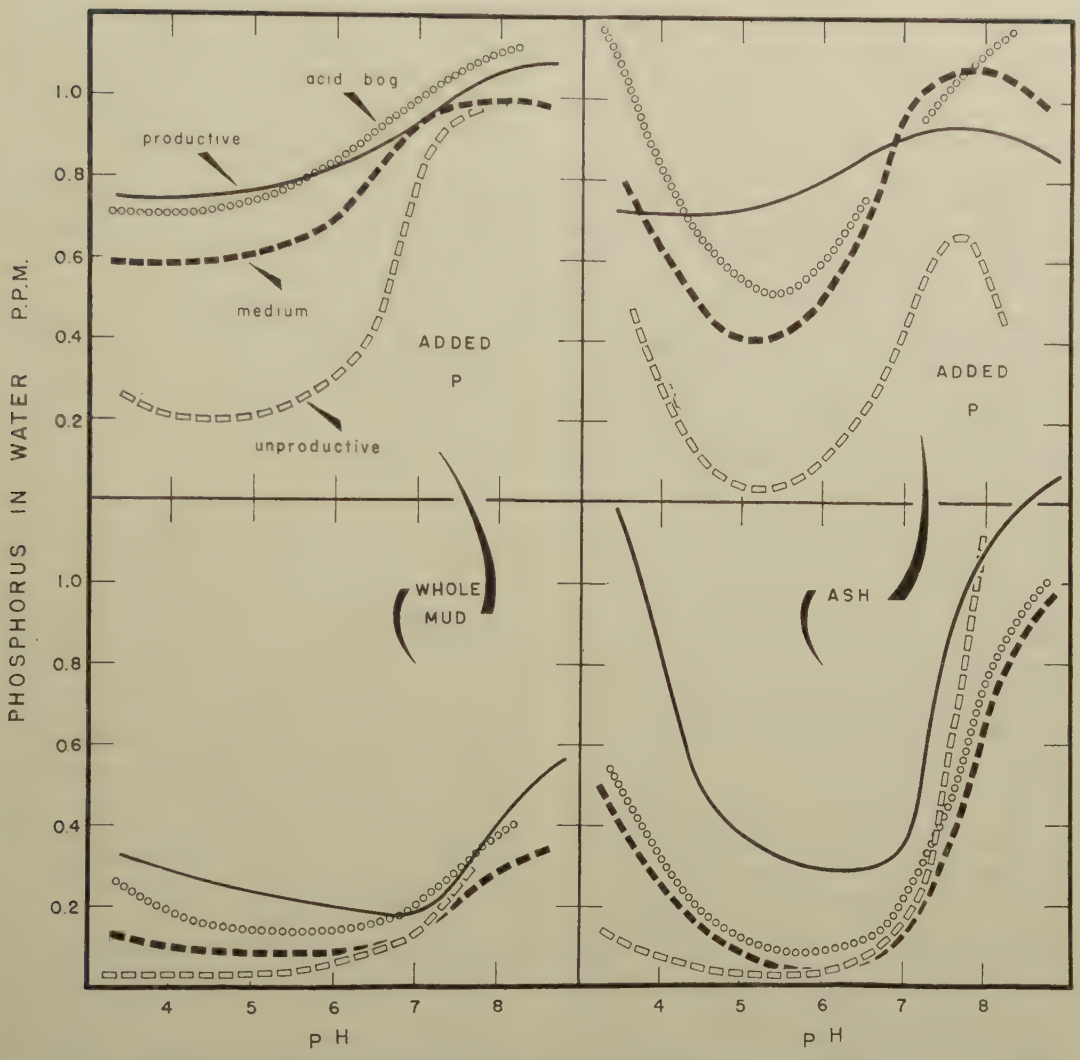


FIG. 3. Superimposed version of Figures 1 and 2. In order to reduce confusion the values for pairs of lakes of each type have been averaged.

superimposed form and, for simplification, with the pairs averaged. The lower left quadrant shows the phosphorus extracted from whole mud by distilled water. It is striking to observe that although the curves deviate somewhat at the acid end, they all reach the same level a little to the right of neutrality. The curves do not go far enough to show clearly whether they deviate again in response to greater alkalinity, but we regard the evidence from the whole of Figure 3 as against such deviation up to pH 9.

Looking at the upper left quadrant (added P) it is again evident that deviation between lake types is associated with an acid reaction, the differences being eliminated at about the neutral point. The lower right illustration (ash versus water) again shows curves that are scarcely distinguishable under alkaline conditions, while at top right (added P) the same is true except for the lowest (unproductive) curve. Too much should not be made of the low right side of this last which may be an error.

The whole of Figure 3 and especially the top right part suggests a levelling off or even downward turn beyond pH 8. This strengthens the doubt already expressed as

to whether a further increase in alkalinity would be accompanied by appreciable release of additional phosphorus to the water.

It is of interest to inquire whether the effects described can be explained as adsorption of phosphate on suspended solids, a topic which has received considerable study by Ohle (1953) and Carritt and Goodgal (1954). Ohle shook up aerated water containing phosphate with a laboratory preparation of $Fe(OH)_3$ gel, and determined what percentage of phosphate was removed at various pH levels. Carritt and Goodgal measured the equilibrium reaction between dissolved phosphate, containing the radiotracer, and several solids including Chesapeake Bay sediments, Fuller's earth (hydrated magnesium and aluminum silicates), and Bentonite (impure aluminum silicate).

In Figure 4 these artificial systems are compared with the mean Copper-Lily ash results, which are selected because they provide the closest resemblance. The trough appears to be at about the same pH in all four curves, and the acid and alkali reactions are also very much alike. A comparison of

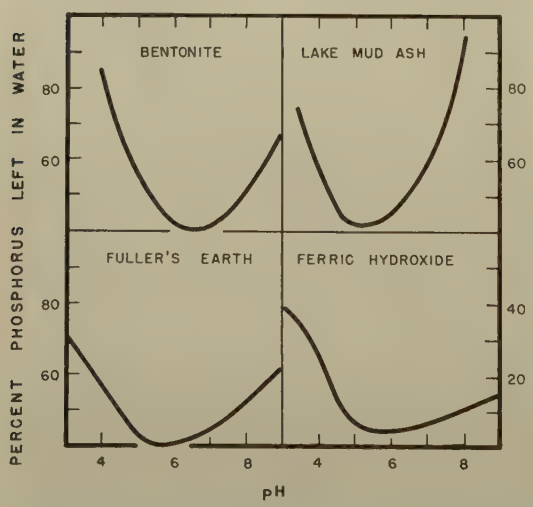


FIG. 4. Comparison of several phosphorus equilibrium curves. Lake ash curve as in upper right quadrant of Figure 3 (medium productivity). Bentonite and Fuller's earth from Carritt and Goodgal (1954). Ferric hydroxide from Ohle (1953), and with ordinate base different from the others. Considering that different procedures, concentrations, and equilibration times were used, the agreement in the form of the curves is surprisingly good.

TABLE 2. *Test leading to the conclusion that pH effects are reversible*

Comparison of phosphorus in equilibrated distilled water control with the same pH reached by acid shaking followed by alkali shaking, or vice versa. The first three columns of figures are essentially alike and they differ from the alkali column. Ten ml of 0.01N HCl or NaOH constituted a treatment. Figures are optical densities, corrected for turbidity, and are proportional to phosphorus in solution.

| Lake & material | Control | Acid + alkali | Alkali + acid | Alkali |
|---|---|---|---|---|
| Grand, whole mud | .056 | .055 | .089 | .303 |
| Grand, ash | .092 | .034 | .054 | 1.032 |
| Silver, whole mud | .218 | .203 | .236 | .345 |
| Silver, ash | .103 | .060 | .032 | 1.052 |
| Southport, whole mud | .183 | .246 | .297 | .462 |
| Southport, ash | .279 | .238 | .325 | .986 |

Figure 4 with phosphoric acid dissociation curves indicates that maximum uptake by solids (the trough) occurs in the pH range in which the singly charged $H_2PO_4^-$ ion is predominant. To sum up, it appears that phosphate may be adsorbed onto various naturally occurring solids in lake sediments including magnesium silicate, aluminum silicate, and ferric hydroxide. Differences between lakes, as in Figures 1 and 2, may be accounted for as variations in the ratios between these and other participating solids.

Table 2 shows results of a test to see whether the pH effect was reversible. With materials at the usual strengths, the pH was raised, or lowered, and after shaking for an hour, brought back to the initial level and again shaken. The amount of water at the start was arranged so that there would be 50 ml at the end. Examination of columns 2, 3, and 4 of the table shows that, while there was on occasion considerable scatter, neither the addition of acid nor alkali, followed by neutralization, produced a general kind of difference from the controls in either whole mud or ash. For comparison the effect of alkali alone is shown in Column 5, being at quite a different level.

## DISCUSSION

The underlying mechanism of phosphate exchange, as seen in ash, appears to be inorganic and reversible. Both these qualities, as well as the general shape of the pH curve,

are characteristic of several naturally occurring solids. Adsorption data are often represented by the empirical equation of Freundlich

$$y = kx^n$$

which Einsele (1938) applied to ferric hydroxide gel, where $y$ is the P concentration in the water (parts per billion) and $x$ is the P adsorbed on the gel (mg per gm Fe). The constants $k$ and $n$ had respective values of 0.01 and 2.5 in a given experiment at pH 7.5.

The equation, according to Einsele, is not quantitatively applicable to conditions of nature for several reasons: the inorganic P in solution in lakes is too small to furnish appreciable amounts for adsorption, being often at the limits of detection, of the order of 1 ppb. The fraction of the iron in the form of ferric hydroxide is unknown. The adsorptive behavior of $Fe(OH)_3$ depends on how it was prepared, *e.g.*, a sample made from ferric chloride will take up more P than one from a ferrous salt.

Further doubt about comparisons of the performance of iron in the laboratory with behavior in nature is furnished by Bloomfield (1952), who found that water extracts of leaves, bark, and pine needles cause non-biological solution of relatively large amounts of hydrous ferric and aluminium oxides. The ferric oxide was reduced to the ferrous state, and continuous aeration of the reaction mixture had no effect on solution or reduction.

The muds from different lakes varied in their inorganic content which ranged from 43 to 84 per cent. The four types selected as pairs were not always close; thus Silver with 65 per cent ash and Punchbowl with 43, are both acid bog types and lie only a few miles apart. Bluff, in the same area and primitive, has 58 per cent. No relation could be seen between the shape of the graphs, or the difference in behavior between whole mud and ash, and the inorganic content. Doubtless a more important factor is the amount of adsorber present, and with iron, the fraction which is in the form of ferric hydroxide. As Einsele has pointed out, when water containing ferrous phosphate in solution is treated with oxygen, the first reaction is the formation of insoluble ferric hydroxide. It is to this iron that any inorganic phosphate, introduced later, would become attached.

In another paper of this series it is shown that when inorganic phosphate is added to water a large part is likely to be quickly converted to an organic form by bacteria. If bacteria are blocked, a rapid absorption by plants takes place instead. Hence under conditions of nature only a minor fraction is likely to be left for the mud adsorption reaction here considered. An opinion about the degree of participation of this residual part can be formed by examination of the upper left quadrant of Figure 3, which shows that at pH 7 or above, practically the whole of the added 1.0 ppm of P failed to be removed by the mud. It might be emphasized that a pH of 8 or more is quite ordinary and natural to non-granite-region limnologists. Even at pH 6 (except for the unproductive pair of lakes) most of the P remained in solution, and increased acidity made little further difference. It is therefore probable that the removal of added phosphorus from oxidized water by adsorption is of minor importance to lake economy. As to reduced water, Einsele has shown that there the inorganic reaction operates in the opposite direction, to liberate P from mud to water. This also, as will be shown elsewhere, appears to be subsidiary to effects brought about by living organisms. Also of course, it can only take place in that part of the lake where the mud surface is reduced, which generally represents from zero to a small fraction of the lake bottom area and is always a part where minimal mixing occurs.

In view of results to be reported in paper IV of this series, it was thought prudent to check the effect of microorganisms on the phosphorus exchange. If bacteria, etc. were causing the mud response, their elimination might be expected to give to whole mud, the behavior of ash, or otherwise to alter the response. Tests were made like those illustrated in Figure 2, but prior to which the dried mud and also the ash were sterilized at 170°C, and the liquids to be used were autoclaved. Tests were done with three lakes—

Bluff, Punchbowl, and Southport. The curves could not be shown to differ from those of Figure 2. Hence no microorganism effect is demonstrated and the present experiments are to be interpreted as descriptions of non-living equilibria. Results might have been positive had fresh mud been used instead of dried and reconstituted samples, or had a longer test period been allowed. Thus Carritt and Goodgal (1954) report that with fresh marine sediments phosphate is adsorbed very rapidly at first then taken up more slowly, presumably by a diffusion reaction. A log-log plot of time versus P taken up is observed to be linear. This relation predicts infinite capacity of the solids, an unreasonable proposition to a chemist but a rather ordinary one to a bacteriologist.

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# Primary Production of Continental Shelf Waters off New York[1]

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ABSTRACT

The chlorophyll-radiation method of measuring primary production, described earlier by the authors, was employed on six oceanographic cruises during 1956–7, each occupying 25 stations across the continental shelf off New York. The relationship photosynthesis/hour (opt. light):chlorophyll *a*, using the oxygen production method, was found to agree with that determined earlier from culture and harbor water experiments, despite wide variations of temperature, nutrients, and the abundance of phytoplankton. The same ratio, with photosynthesis measured by $C^{14}$ uptake, was extremely variable and usually lower than that obtained by oxygen-production photosynthesis values.

Estimates of daily production beneath a square meter of sea surface by the chlorophyll-radiation method and *in situ* $C^{14}$ values agreed within reasonable limits in 75% of the measurements; for the remainder of the times the $C^{14}$ values were consistently lower.

Daily production throughout the year ranged roughly from 0.20 to 1.00 g carbon/m²/day within the whole area studied. Estimated annual production decreased in a seaward direction from 160 g carbon/m²/year in the shallow coastal waters to 100 g carbon/m²/year on the continental slope. These values are intermediate between Riley's estimates for Long Island Sound and the Sargasso Sea.

## INTRODUCTION

The authors have recently described a method of estimating the rate of primary production by phytoplankton from measurements of chlorophyll, light penetration, and incident radiation (Ryther and Yentsch 1957). During the past year we have investigated this method further and have employed it routinely, whenever possible in conjunction with the $C^{14}$ and "light and dark bottle" oxygen techniques. These studies were carried out as part of an investigation of the plankton ecology of the continental shelf region off New York. The measurements of productivity in themselves represent a minor part of the total effort of this investigation. They are presented here primarily to demonstrate the use and to some extent the reliability of the above-mentioned new technique throughout a period of a year and in waters where production varies widely both seasonally and geographically.

[1] Contribution No. 906 from the Woods Hole Oceanographic Institution. These studies were carried out under Contract AT(30-1)-1918 with the U. S. Atomic Energy Commission and with the partial support of Research Grants G-3234 and G-2650 from the National Science Foundation. The authors wish to acknowledge the help provided by E. M. Hulburt, G. C. McLeod, W. H. Sutcliffe, D. W. Menzel in the field, Mrs. R. W. Kahler in the laboratory analyses, and B. H. Ketchum in reviewing this manuscript.

## CRUISE PLAN AND METHODS

Productivity measurements have been made at 25 stations in the continental shelf area off New York. These stations are arranged in a triangle, two sides of which constitute sections across the shelf in depths of water ranging from about 50 to 2000 meters. The inshore end of one section is opposite Montauk Point, Long Island; that of the other is near Barnegat Lightship off the New Jersey coast. The third leg of the triangle connects these inshore stations and is laid out closely parallel to and slightly inside the 50-meter contour. The location of these stations is shown in Figure 1.

At each station of 100 meters or more of depth water samples were collected with a plastic-lined sampler from depths of 0, 10, 25, 50, 75, and 100 meters. At stations of less depth, samples were collected from 0, 10, and 20 meters and thereafter at 20-meter intervals to the bottom. Normally two-liter samples from each depth were millipore filtered and subsequently analyzed for plant

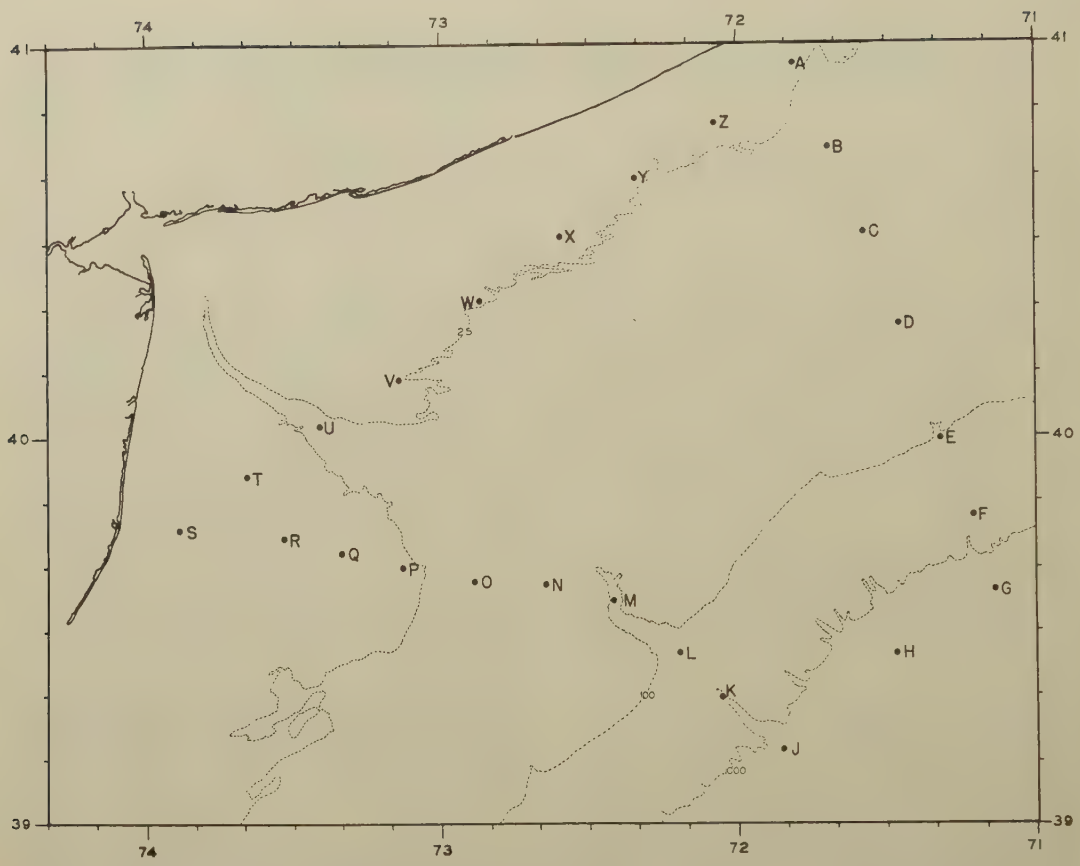


FIG. 1. The continental shelf area off Long Island and New Jersey showing station locations. Depth contours in fathoms.

pigments according to the method of Richards with Thompson (1952) as modified by Creitz and Richards (1955). When phytoplankton was scarce, two casts were made and 4 to 5 liters of water were filtered.

Water from the 10-meter sample was dispensed into two transparent and two darkened bottles, one of each receiving approximately 3 $\mu$curies of $C^{14}O_3^=$. All four bottles were then placed in an incubator cooled with running sea water and illuminated with ten 15-watt fluorescent lamps, which provided a light intensity incident to the bottles of 1500 foot-candles.

The samples containing $C^{14}$ were removed after 12 hours, filtered, and productivity calculated according to the method of Steemann Nielsen (1952) except that the dark uptake of $C^{14}$ was routinely subtracted from that observed in the light and no correction was made for respiration.

The other pair of light and dark bottles was removed from the incubator after 24 hours, their oxygen concentration determined by the Winkler method, and photosynthesis (expressed as carbon fixed) calculated from the difference between them, using an assimilatory quotient ($O_2/CO_2$) of 1.25 (see Ryther 1956a).

During each cruise *in situ* $C^{14}$ measurements were also made, weather permitting, at one shallow station (<50 meters), one deep station (>1000 meters), and one station of intermediate depth.

For these measurements light and dark bottles with $C^{14}O_3^=$ added were filled with the water samples taken from each depth to 100 m or to the bottom. These were then

fastened to a wire, suspended at the depths from which the samples were taken, and exposed to natural illumination, usually from sunrise to noon, occasionally from noon to sunset or from sunrise to sunset. The samples were processed, and productivity was calculated in the same way as for the incubator-exposed $C^{14}$ samples.

Light penetration was measured at each station occupied during daylight with a submarine photometer. The mean extinction coefficient of daylight was calculated over the depth to which 1% of the surface light penetrated. Where direct photometry could not be employed due to unfavorable weather or limitation of time, secchi disc readings were converted to values for extinction coefficient using the relationship

$$k = \frac{1.7}{\text{Secchi disc}}$$

as proposed by Poole and Atkins (1929), which was consistent with our measurements where both methods were employed. Extinction coefficients for stations occupied at night were estimated by interpolation between stations where measurements could be made in daylight.

The daily rate of primary production ($mgC/m^3/day$) was calculated for five depths from chlorophyll *a*, light penetration, and incident radiation using the equations given by Ryther and Yentsch (1957). This was done for every cruise and at every station. These values, and those obtained from *in situ* $C^{14}$ measurements, were plotted against depth and graphically integrated to give daily production on an areal (square meter) basis.

Normally radiation values used in these calculations were taken from Kimball's (1928) tables, so that production is expressed in terms of average or normal radiation for the area studied and the particular time of year in question. However, at those stations and times when *in situ* $C^{14}$ experiments were conducted simultaneously, in order that the two methods could be compared, production was calculated from radiation values which were actually measured using either a recording Epply Pyrheliometer or a G. E. Radiation Meter.

The measurements which will be presented in this paper were made during six cruises in the months of September, December, February, March, May, and July, and will thus give a rough picture of the annual cycle of primary production in these coastal waters.

## THE RELATIONSHIP BETWEEN PHOTOSYNTHESIS AND CHLOROPHYLL *a*

In the earlier studies already referred to the relationship between photosynthesis at optimum light intensity and chlorophyll *a* was determined using natural plankton populations from the Woods Hole region and cultures of marine phytoplankton. The results of these experiments and some values from the literature were used to calculate a mean value of 3.7 grams carbon assimilated per hour per gram of chlorophyll *a*.

Figure 2A shows the ratio of photosynthesis per hour at optimum light and chlorophyll *a* as determined from the 10-meter samples collected at each station during the six continental shelf cruises. The open circles represent values obtained by the "light and dark bottle" oxygen method; the closed circles are values obtained by $C^{14}$ uptake. The data are plotted as a log function so that both high and low ratios will appear equally weighted on the graph. There is still some bias in favor of high ratios obtained by the oxygen method, however, since with large positive differences between light and dark bottles, one cannot distinguish between experimental error and high photosynthesis, and the data are therefore included, while negative differences (more oxygen in the dark than in the light bottles) were recognizable as experimental error and discarded. The absence from the graph of values obtained by the oxygen method indicates either that such measurements were not attempted (*i.e.*, during the first two cruises) or that significant results were not obtained.

The line drawn through Figure 2A represents the 3.7 ratio obtained in the earlier experiments described above. The points

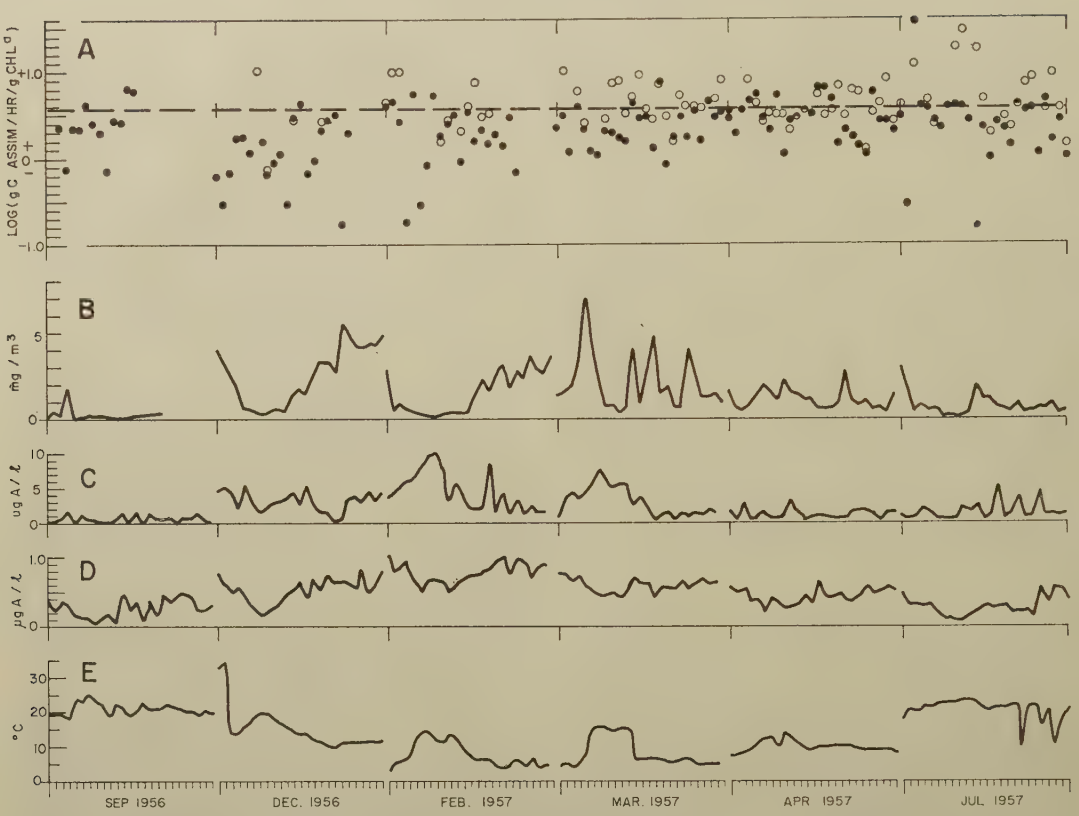


FIG. 2. Biological, chemical, and physical properties of water from 10 meters depth shown for all stations occupied during six continental shelf cruises. Station data presented for each cruise in alphabetical order (A–Z) as stations were occupied. (*A*) Log ratio photosynthesis/hour (optimum light): chlorophyll *a*. Open circles, oxygen method; filled circles, $C^{14}$ method. (*B*) Chlorophyll *a* concentration. (*C*) Available nitrogen ($NH^+ + NO_2^- + NO_3^-$). (*D*) Phosphate. (*E*) Temperature.

obtained by the oxygen method appear to be distributed rather evenly about this line despite their high degree of scatter. This is more obvious if one looks at the frequency distribution of the ratios in Figure 3A, which shows a decided peak of values ranging from 3.0 to 4.0 and a normal distribution of ratios about this mode.

In our earlier report, we acknowledged that the value 3.7 was no more than the mean of some highly variable data, and that there was little reason to assume that it would be constant under all conditions. The data presented here certainly show no less variability. However, there is no obvious effect of environmental conditions upon the ratio despite rather wide variations in the abundance of phytoplankton (*i.e.*, chlorophyll *a*), the concentration of available nitrogen and phosphorus, and temperature (Figure 2B, C, D, and E). This is a hopeful indication that most of the scatter of our observations is due to experimental error. Unless this error is systematic in nature, the mean would appear to assume greater reliability than we had originally hoped for.

The values obtained by the $C^{14}$ method are obviously scattered for the most part below the 3.7 line, as emphasized again by their frequency distribution (Fig. 3B.). Furthermore they show no obvious normal distribution about a mean, as do the oxygen values, but appear to be almost equally spread between values of 1.0 and 4.0, and with a considerable number below 1.0. A similar variability in the relationship between chlorophyll *a* and $C^{14}$ uptake has been reported by Holmes *et al.* (1957), Holmes

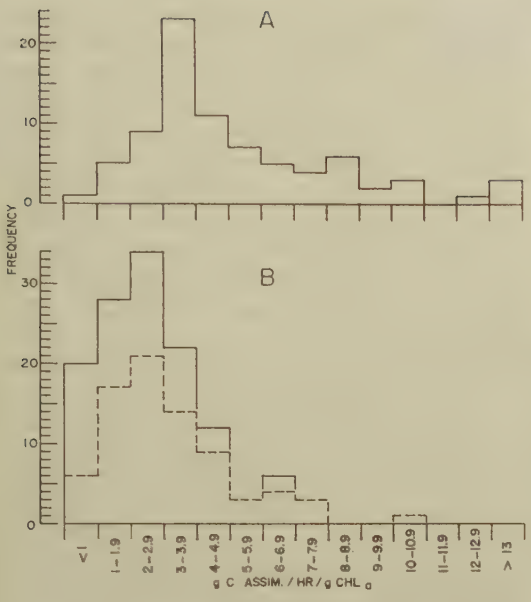


FIG. 3. Frequency distribution of the ratio photosynthesis per hour (opt. light):chlorophyll *a* for values given in Figure 2A. (*A*) Oxygen method. (*B*) $C^{14}$ method. Broken line in (*B*) represents those $C^{14}$ values which were obtained simultaneously with the oxygen method values shown in (*A*).

(in press), Doty (unpublished data), Currie (in press), and others. We have interpreted this fact on the basis of our contention that the ratio photosynthesis:respiration in marine phytoplankton is not constant (Ryther 1954; Ketchum *et al.*, in press). If this is true and $C^{14}$ uptake, uncorrected for respiration, is a measure of net photosynthesis (Ryther 1954, 1956a, 1956b), then the ratio of $C^{14}$ uptake:chlorophyll should not be constant and should fall below 3.7 by an amount equivalent to respiration. The fact that these ratios are quite variable and are, for the most part, less than 3.7 is consistent with this hypothesis. There is some indication that the highest $C^{14}$:chlorophyll ratios existed during the spring when they closely approached the 3.7 value, indicating that net and gross production (at optimum light conditions) were almost equal. At that time of the year the standing crop of phytoplankton and its *in situ* rate of production were also highest as will be shown in the following section.

## THE COMPARISON BETWEEN *in situ* $C^{14}$ MEASUREMENTS AND PRODUCTION CALCULATED FROM CHLOROPHYLL AND RADIATION

Figure 4 shows the values for production integrated over the euphotic zone and expressed in grams carbon/$m^2$/day for all stations and for the six cruises between September 1956 and July 1957. The clear bar graphs are values calculated from chlorophyll and radiation. The dark bars are the

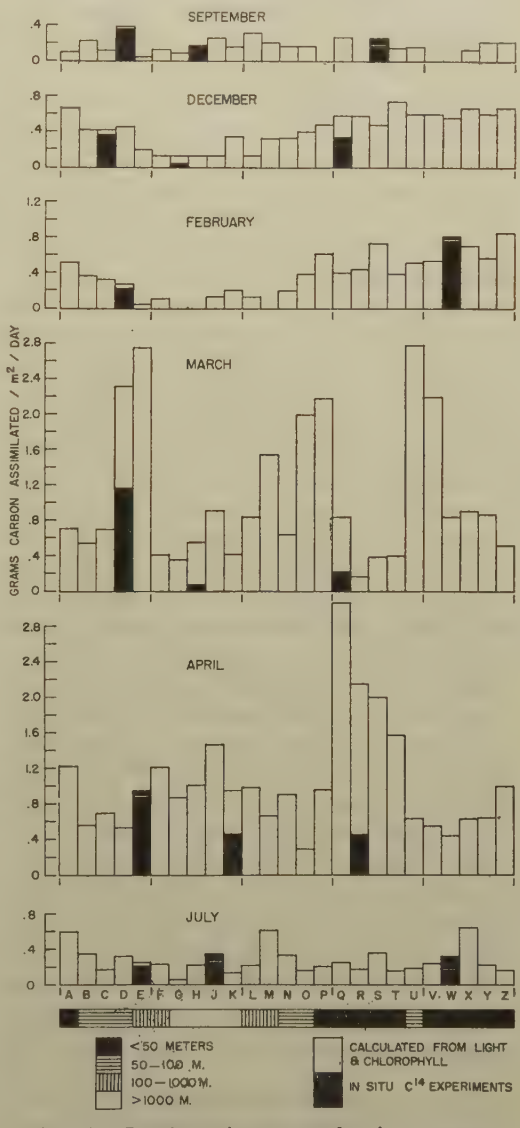


FIG. 4. *In situ* primary production measured by $C^{14}$ method and/or calculated from chlorophyll, radiation, and light penetration for all stations occupied during six cruises.

*in situ* $C^{14}$ measurements. For each cruise the data are presented chronologically in the order in which the stations were occupied (*i.e.*, A–Z). No attempt has been made here to depict seasonal or geographical variations, which will be discussed in the following section, but this complete presentation of data will illustrate the magnitude and range of production, its relation to water depth, and its variability from station to station. However, the main purpose of the figure is to show the comparison between values calculated by the chlorophyll and the *in situ* $C^{14}$ methods.

Of the 17 pairs of data obtained by the two methods, five agree within 10% and all but four differ by less than two-fold. Since the chlorophyll and $C^{14}$ methods measure gross and net production respectively, some difference between them is to be expected. It is true that where there is a big discrepancy, the $C^{14}$ method consistently gave the lower values. But the cases in which the two methods agree and disagree do not seem to be in accord with other evidence. In July and September, when the water was thermally stratified, nutrients low, and the crop of phytoplankton at its minimum, the greatest discrepancy between net and gross production might be expected. At those times the $C^{14}$ and chlorophyll methods gave comparable results, with the former often the higher. On the other hand, during the spring flowering net and gross production should be nearly equal; yet in March and April when production was highest, the greatest discrepancy between the two methods was observed. We do not yet understand this apparent inconsistency, which may result from some systematic error in either method. It is virtually certain that such errors exist, in sampling and technique as well as in the assumptions upon which the calculations are based. Until these are eliminated, or at least assessed, there can be little significance attached to differences between values obtained by the two methods.

## SEASONAL AND GEOGRAPHICAL VARIABILITY OF PRIMARY PRODUCTION

It is difficult to construct a picture of the annual cycle of primary production with data obtained from six cruises. However, the times of these cruises were chosen so as to coincide with the periods of most rapid change or greatest contrast in biological activity. To the extent that these were wise choices, some idea may be had of the seasonal trend and annual range of production. Similarly, geographical variability may be examined within the area studied, which again was chosen for its contrasting features particularly with respect to water depth.

These temporal and spatial trends are somewhat obscured by the high degree of variability of data from one station to the next during any one cruise (see Fig. 4). Judging from the variability of other chemical and biological parameters (Fig. 2), there is reason to assume that this erratic distribution actually exists, though it may be exaggerated by experimental error. The resulting rather confusing picture may be improved by averaging the results from several geographically similar stations. This was done for five shallow, inshore stations (A, S, U, W, Y), five stations of intermediate depth (B, C, D, O, N), and five stations of greater than 1000 meters depth (F, G, H, J, K). Productivity data used in this discussion are limited to measurements obtained by the chlorophyll method. The results are illustrated in Figure 5.

It may be seen that the annual range of production does not differ appreciably between the inshore and offshore locations, 0.20–0.85 g carbon/$m^2$/day for the former and 0.10–1.10 g carbon/$m^2$/day for the latter. It is interesting to compare these values with Riley's most recent estimates of production in Long Island Sound (Riley 1956) which, when converted to carbon assimilation by the method used above, indicate a range of 0.23–1.70 g carbon/$m^2$/day for 1952–3 and 0.24–1.51 g carbon/$m^2$/day for 1953–4. His calculations are based upon *in situ* chemical changes in the water column over periods of several weeks, and such long-term averages obscure extremes which may persist for a few days only. On the other hand, there is no reason to assume that the six continental shelf cruises (comprising in all about one month out of the year) would

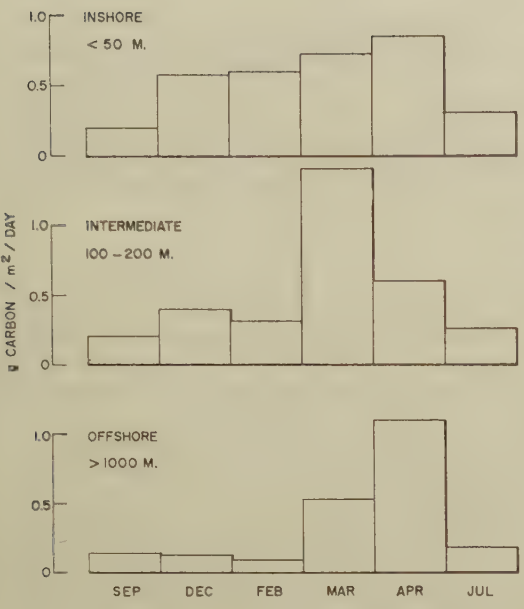


FIG. 5. Mean daily primary production beneath a square meter of sea surface at five shallow, five intermediate, and five deep stations for each of six cruises.

coincide exactly with the period of maximum and minimum production, even though they were chosen with this object in view. Thus we may tentatively conclude that the annual range of production is about the same from Long Island Sound across the adjacent continental shelf to the slope waters. Extending the comparison to truly oceanic conditions, we may again refer to Riley (1957) who has recently made new estimates of primary production in the north central Sargasso Sea. His values for gross production range from 0.09 to 0.89 g carbon/m²/day, again strikingly similar to the range observed in the other regions discussed above.

This similarity in the annual range of production is not surprising, for it simply illustrates the fact that throughout the oceans enrichment processes exist, at times of sufficient magnitude that nutrient concentrations do not limit photosynthesis, at other times so weakly developed that organic production is probably largely dependent upon regeneration of nutrients within the euphotic layer. This, of course, does not imply that total annual production is comparable in these different parts of the sea. It is rather obvious from Figure 5 that this value is higher in the inshore area than in the shelf or slope waters, due to the persistence of relatively high production in the shallow waters throughout the winter and spring in contrast to the spring flowerings of greater magnitude but of briefer duration which occurred in the deeper waters.

The fact that the onset of the spring flowering in temperate latitudes is earlier in shallow and later in deep waters, and the explanation for this phenomenon, has been dealt with by Sverdrup (1953), Riley (1957), and others and need not be discussed in detail here. In brief it involves the interrelationship between the depths of the euphotic and mixed layers (*i.e.*, Sverdrup's critical depth) which determines the average light intensity to which the phytoplankton community is exposed. Since shallow coastal waters are mixed to the bottom in wintertime, the average light intensity within the water column is inversely proportional to its depth, and in sufficiently shallow waters the average plant cell within the water column receives adequate light for production throughout the year. In such places the plants have access to the nutrients dissolved within the entire water column and regenerated from the bottom, photosynthesis is limited by light only, and production can persist at a moderately high level throughout the winter and spring, and until thermal stratification imposes a barrier between the illuminated plants in the upper water and the reservoir of nutrients in the deep water and the bottom. Following the development of the thermocline there may be a brief period of high production, since the average cell above the thermocline is now exposed to much greater radiation. But the limited supply of nutrients in these surface waters is then quickly exhausted, and photosynthesis is reduced to a low level throughout the summer and until cooling and mixing processes again destroy the thermocline.

In contrast to the situation described above, the offshore waters are mixed in winter to a depth of 200 m or more, and the average plant cell within this water column

does not receive sufficient light to grow. Here production exists at a low level throughout the winter and until thermal stratification retains the cells in the upper water layer. There then follows the classical spring flowering which may be of greater magnitude than that occurring in the shallow waters (see Fig. 5), since the nutrients have not been depleted by growth during the winter. As in the shallow water this activity rapidly exhausts the supply of nutrients from the surface waters, and low summer production ensues, perhaps punctuated by minor flowerings resulting from the temporary breakdown of the thermocline through local storm action, as described by Riley (1957).

Thus daily photosynthesis in the open sea may equal or exceed that of shallow coastal waters, but high levels of production in offshore waters cannot be sustained over long periods, as they may be inshore, unless there exist mechanisms such as upwelling for the continued enrichment of the surface waters. Except in these cases the annual production of the oceans must be considerably lower than that of shallow coastal waters 50 meters or less in depth.

As mentioned earlier, no accurate calculation of annual production may be made from six scattered points. But a rough and rather subjective estimate (obtained by drawing a smooth annual curve through the points) is of some interest, particularly when compared with Riley's values for Long Island Sound and the Sargasso Sea. For the sake of consistency, the latter have been recalculated from Riley's data using an assimilatory quotient of 1.25 in converting from oxygen changes to carbon fixation. The results, presented in Table 1, show that annual production decreases in a seaward direction, as discussed above, the variation across the continental shelf being relatively small and the values for that region being intermediate between those for Long Island Sound and the Sargasso Sea.

TABLE 1. *Annual rate of carbon fixation, in grams per square meter of sea surface*

| | Total depth (meters) | gC/m²/yr |
|---|---|---|
| Long Island Sound | 25 | 380 |
| Continental Shelf | 25–50 | 160 |
| | 50–1000 | 135 |
| | 1000–2000 | 100 |
| North Central Sargasso Sea | >5000 | 78 |

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# Diurnal Fluctuation in Photosynthetic Rate and Chlorophyll "a" Content of Phytoplankton from Eastern Pacific Waters

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ABSTRACT

Measurements were made of photosynthetic activity and chlorophyll "a" content of phytoplankton samples taken at regular intervals over a 46-hour period in May 1957, from surface waters near Clarion Island in the eastern Pacific Ocean. Results confirm previous observations of a diurnal periodicity in photosynthesis which, in this particular instance, appears to be correlated with variations in chlorophyll content. The photosynthesis-chlorophyll relationship gives an estimated value of 4.24 mg C/hr per mg of chlorophyll "a" at a light intensity of 1000 foot-candles.

## INTRODUCTION

The Inter-American Tropical Tuna Commission in cooperation with the University of California Scripps Institution of Oceanography undertook from May 8 to June 12, 1957, an expedition to Clarion Island (18°21′ N. lat., 114°44′ W. long.), an important tuna fishing area in the Revilla Gigedo Islands southwest of Baja California. The primary objective of this cruise was to determine the manner in which a small isolated land mass, such as Clarion Island, may modify the surrounding oceanic environment and so create conditions which are attractive to aggregations of pelagic fish, particularly the tunas. Incidental to the comprehensive chemical, physical, and biological work relating to this program which was conducted aboard the Scripps research vessel SPENCER F. BAIRD, a study was made of the rate of carbon fixation and variations in chlorophyll "a" content of phytoplankton samples taken at regular intervals from surface waters at a fixed position over a 2-day period. Results indicate that phytoplankton collected from the ocean surface near Clarion Island exhibit a diurnal photosynthetic periodicity similar to those described by recent investigators (Doty and Oguri 1957, Yentsch and Ryther 1957, Holmes and Haxo 1957), and that the rate of carbon fixation at a given time appears to be related to the total amount of chlorophyll "a" present in the water sample.

The author wishes to acknowledge the assistance of Messrs. Richard C. Hennemuth and James A. Renner of the Commission staff. Appreciation is also extended to Mr. Robert W. Holmes and his associates at the University of California Scripps Institution of Oceanography for providing some of the essential materials and equipment used during the expedition.

## METHODS AND MATERIALS

Commencing at 1500 Pacific Standard Time, on May 28, the BAIRD occupied for a 72-hour period hydrographic station No. 47, situated about one mile offshore from the southwest corner of Clarion Island, in approximately 200 fathoms of water. A buoy was anchored at this locality to serve as a fixed reference point to which the drifting vessel could return for hourly observations. Sampling of surface waters at the reference buoy to study short-term variations in the photosynthetic rate and chlorophyll "a" content of phytoplankton present in the area began at 1600 PST on May 28 and was concluded 46 hours later. During this period, surface samples for carbon uptake measurements were collected every two hours by means of a plastic bucket; samples for chlorophyll "a" determinations were obtained in the same manner at four-hour intervals. When samples for both analyses were taken simultaneously, to ensure that the phytoplankton content was as nearly homogenous as possible the surface water was poured into an 8-liter plastic bottle and shaken before

the necessary aliquots for carbon work were drained off. Six liters of the remaining water were taken for chlorophyll filtration.

The techniques employed to measure carbon fixation by means of a radioactive isotope, carbon 14, followed those developed by Steemann Nielsen (1952). Laboratory procedures were generally as follows:

Three 125-ml Pyrex glass bottles were filled with surface seawater at each two-hour interval. Two of these bottles were clear; the third was a "dark" bottle, the body of which was completely covered with black electrical "Scotch" tape and the top wrapped in aluminum foil to prevent the entry of light. The content of each bottle was inoculated with one microcurie of carbon 14, and the bottles were then placed in a seawater bath and exposed to a bank of 12 daylight-type fluorescent tubes. The temperature at which each sample was incubated was approximately equal to or slightly higher (one degree at most) than that of the surface water at the time the sample was taken. Sea-surface temperatures ranged from 23.9° to 25°C during the course of the experiment. The samples were incubated for 6 hours (in two cases for 4 hours) at light intensities varying from 960 to 1100 foot-candles measured at the surface of the bottles.

At the end of each incubation period the content of each bottle was filtered through an HA Millipore filter. The filter was then dried in a vacuum desiccator and the activity was subsequently counted in a proportional-flow counter. The mean count of each pair of samples was converted to milligrams of carbon fixed per hour at a standard light intensity of 1000 foot-candles, assuming that the total carbon dioxide concentration of seawater was 90 milligrams per liter, and disregarding the "isotope effect." Dark

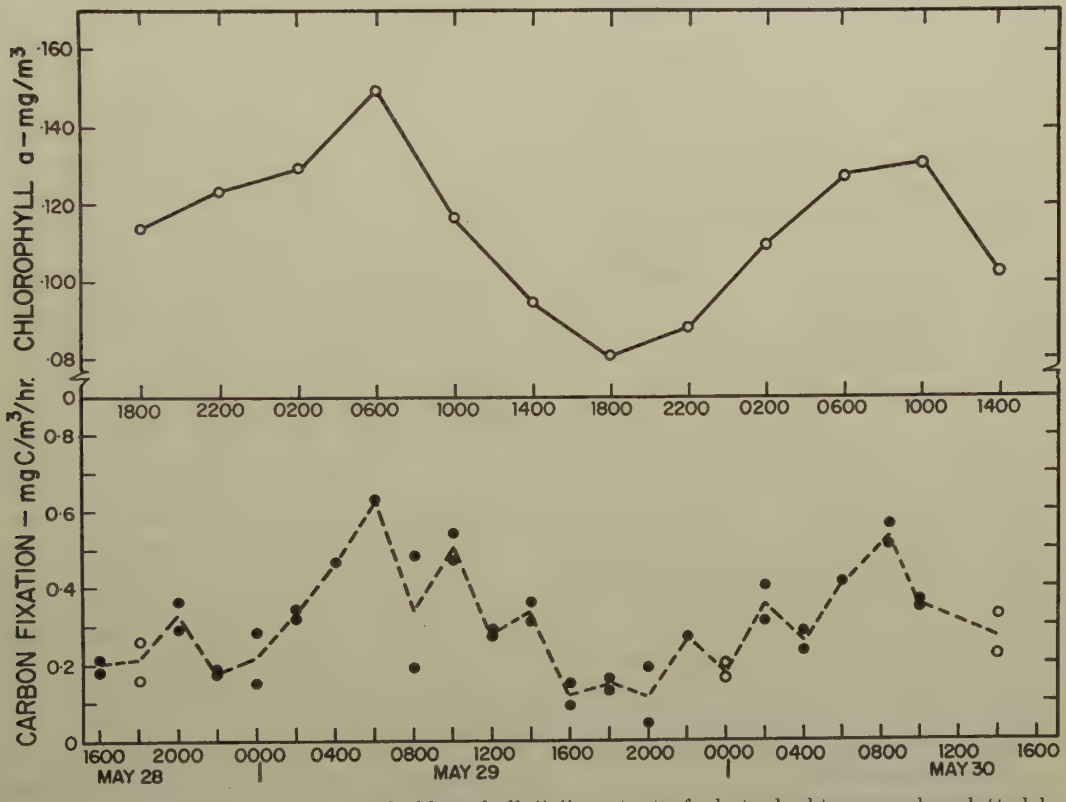


FIG. 1. Photosynthetic rates and chlorophyll "a" content of phytoplankton samples plotted by time of collection from surface waters near Clarion Island, May 28–30, 1957. Solid circles in lower panel represent observed net carbon fixation rates; open circles denote observed light-bottle uptakes corrected for non-photosynthetic activity by mean dark-bottle assimilation of $C^{14}$.

bottles were used to estimate non-photosynthetic fixation of carbon dioxide.

The methods of measuring the amount of chlorophyll "a" present in marine phytoplankton have been outlined by Richards with Thompson (1952) and Creitz and Richards (1955). At each experiment interval of four hours, a six-liter sample of surface seawater to which a trace amount of a buffering agent, magnesium carbonate ($MgCO_3$), had been added, was filtered through an HA Millipore filter. The filter was placed in a 12-ml Pyrex test tube to which was then added 3 ml of 90 per cent glass-redistilled reagent-grade acetone. The chlorophyll was extracted in acetone over a 12-hour period in a refrigerator at approximately 10°C. Subsequently, the extract was centrifuged at 4500 r.p.m. until clear and then decanted into another test tube. An additional 3 ml of acetone were then added to the filter residue, mixed, and centrifuged, and the second extract added to the first. The combined acetone extract of approximately 5–6 ml was re-centrifuged and decanted into a 10-ml volumetric graduate. The extract was diluted to 6 ml, and its optical density was measured in a 10-cm semi-micro absorption cell using a Beckman model DU spectrophotometer. Chlorophyll "a" concentrations were determined from transmission readings made at 635, 645, and 665 mμ, and a tubidity correction at 750 mμ, employing the equations given by Richards with Thompson (1952).

## RESULTS

Although a number of carbon 14 samples were unavoidably lost, the remaining data plotted in Figure 1 give a fairly comprehensive picture of the changes in carbon fixation rate with time and associated variations in chlorophyll "a" content. The photosynthetic rates given in the lower panel represent light-bottle values corrected for non-photosynthetic activity. Where dark uptake was not measured simultaneously, the mean of the measured dark-bottle counts was employed.

The striking feature of these data is the cyclical nature of the variations in photosynthetic activity which occurred over the 46-hour experimental period, and which appears to be closely correlated with changes in chlorophyll "a" content of the phytoplankton. On two successive days the rate of carbon fixation reached a peak in the early morning hours and fell to its lowest level in the late afternoon, with intermediate values occurring between. Associated with this diurnal rhythm were similar coincident fluctuations in chlorophyll "a" values. While the times of occurrence of the maximum and minimum photosynthetic rates do not coincide exactly with those reported by Doty and Oguri (1957), Yentsch and Ryther (1957), and more recently by Holmes and Haxo (1957), they agree substantially with the findings of these investigators. However, neither Doty and Oguri nor Holmes and Haxo found a positive correlation between photosynthesis and chlorophyll "a" concentration. Yentsch and Ryther, on the other hand, encountered this interrelationship in their experiments and have suggested that it may be related, in part, to the diurnal interaction between chlorophyll content and the intensity of solar radiation.

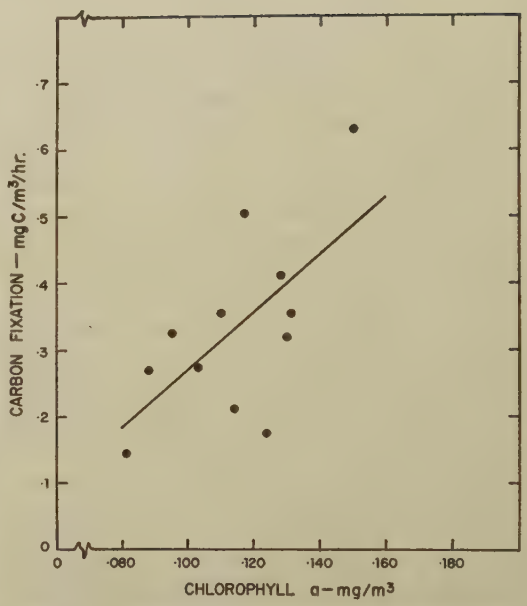


FIG. 2. Relationship between photosynthetic rate and chlorophyll "a" content of phytoplankton samples collected near Clarion Island, May 28–30, 1957. Least-squares line is described by equation $Y = -0.17 + 4.41\ X$, with standard error of estimate of 0.11.

The rate of photosynthesis per unit amount of chlorophyll "a" is of some interest and may be examined from the data given in Figure 2 where net carbon fixation rates (mean light-minus-dark bottle uptake) obtained at 1000 foot-candles of illumination are plotted against chlorophyll concentrations of samples taken at the same time. Although there is some scatter about the least-squares line, the relationship between the two indices appears to be fairly good over the range of values encountered during the experiment, and yields an estimated incubator production rate of 4.24 mg C/hr per milligram of chlorophyll "a". This is intermediate to the production values of 2.5 and 7.3 calculated previously on a comparable basis for tropical Eastern Pacific phytoplankton by Holmes *et al.* (1957). It should be noted, however, that the latter ratios were derived from observations made over a wide region of the Eastern Pacific Ocean, encompassing several areas of different physical and biological characteristics and not from samples of phytoplankton taken at a stationary locality in a particular environment as in the present experiment.

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# Uptake of $P^{32}$ and Primary Productivity in Marine Benthic Algae[1]

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ABSTRACT

The rate of uptake of tracer $P^{32}$ from normal sea water and the primary productivity of seven species of large intertidal benthic algae were measured simultaneously in light and dark bottles suspended in a running seawater aquarium under constant light and temperature. Per cent uptake of $P^{32}$ per hour per gram biomass was similar in the light and dark for a given species, but markedly different between species. In the extremes of the series the relative rate of uptake was 25 times greater in *Cladophora* than in *Fucus*. Both the uptake rate and gross productivity were proportional to the surface-per-volume ratio in the series of species. These data suggested that when environmental concentration of phosphorus is low, as is usual in the sea, it is absorbed at a rate related to the inherent surface area features of the alga, high surface-to-volume ratio increasing the rate of uptake as well as increasing the ability of a given biomass of plant to fix energy under favorable light conditions. Therefore, under these conditions uptake is related to potential productivity and not to the current metabolic level.

## INTRODUCTION

When radioactive phosphorus became generally available it appeared to be a promising tool for applying the "raw material disappearance method" in the study of the productivity of steady-state ecosystems in nature. $P^{32}$ has been invaluable in the study of turnover rates in the phosphorus cycle, as recently summarized by Hutchinson (1957). However, it has not proved to be very satisfactory in the measurement of productivity in short-term experiments, because phosphorus in various forms is readily taken up through sorption by sediments and by organisms without being immediately incorporated into protoplasm. Thus, while $P^{32}$ added to a body of water may be removed from the water at a rate which is related to the community metabolic rate, it has been difficult to distinguish between biological assimilation and "physical uptake." Studies on algal cultures as well as $P^{32}$-tagged fertilizer experiments with land plants have clearly shown that while actively metabolizing organisms are likely to absorb more of the tracer than less active ones within a given period of time, uptake is greatly affected by prior environmental and organismal concentrations of phosphorus, and by varying rates of exchange (*i.e.*, "back diffusion" from organism to medium) with the result that there is often no rigid proportionality between $P^{32}$ uptake rate and metabolic level (Gest and Kamen 1948, Rice 1953, Arnon 1956). It is evident that studies on simplified ecosystems are needed before the disappearance rates of radioactive materials released into complex natural communities can be properly interpreted.

In the present study the simplest possible short-term experiments were carried out designed to compare uptake rate and primary productivity in representative species of large marine algae having different surface-per-volume ratios. These experiments constituted one of the staff-student research projects which were a part of the 1957 Marine Ecology Course at the Marine Biological Laboratory, Woods Hole, Massachusetts. The authors are indebted to Miss Joanne Van Dyk, assistant in the course, for aid in setting up equipment; to Dr. Mones Berman of the MBL Isotopes Laboratory for important suggestions regarding the design of the experiments; and to Dr. Lawrence R. Pomeroy, University of Geor-

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gia, and Dr. Richard F. Foster, AEC Hanford Laboratory, for critical reading of the manuscript.

## METHODS

Experiments were conducted in paired "light" and "dark" (covered with black tape to exclude all light) glass-stoppered bottles of 500 ml capacity suspended in a running sea water aquarium at constant temperature (approximately 21°C). A constant illumination of 450 foot-candles was provided by four fluorescent tubes, two on each side of the aquarium. The bottles were free to swing back and forth in the current, which produced gentle agitation of the contents. Fresh, actively growing pieces of algae were collected from the nearby bay and, within minutes, placed in the bottles in the sea water from the laboratory sea water system (which draws water from the same bay where most of the algae were collected). Seven species, representing all three major groups of marine seaweeds (Chlorophyta, Phaeophyta, and Rhodophyta), and ranging in life form from "filmy" to more massive types were studied as follows: *Fucus vesiculosis*, *Chondrus crispus*, *Ceramium rubrum*, *Sargassum filipendula*, *Chorda filum*, *Ulva lactuca*, and *Cladophora glaucescens*. Approximately one gram dry weight of alga per bottle proved satisfactory for all but the most active species in which cases the amount was reduced to about 0.5 grams in order to prevent too rapid depletion of oxygen in the dark bottle or the formation of bubbles in the light bottle.

One microcurie of carrier-free $P^{32}$ as phosphate was added to each bottle containing the alga, and also to control bottles without algae. Uptake was measured by counting the radioactivity present in samples of the water removed at 0, 0.5, 1.5, 2.5, and 3.5 hours. At each period bottles were removed from the bath, shaken gently to insure thorough mixing, and five aliquots of 0.2 ml each removed with an automatic pipette; the water samples were dried on metal planchets and counted with a conventional end-window Geiger-Müller tube connected with a scaler-of-64 circuit. Since radioactivity of the water in the control bottles did not decline during the experimental period it was concluded that no measurable $P^{32}$ was adsorbed to the surface of the glass. Uptake by microorganisms in the water posed no problem in this simple setup since the sample counted contained a sample of such organisms. Bacteria in the water probably converted some $P^{32}$ into organic form thus rendering it unavailable for exchange by the algae, but this should not affect the relative rates of uptake by the latter. Finally, while seaweed with macroscopic epiphytes was not used, any film of bacteria or other microscopic "Aufwuchs" on the algae was considered to be a normal part of the plant taken as an ecological unit. Thus, any loss of radioactivity in the water was assumed to represent a corresponding gain by the algal unit. Several experiments of the same type were also run using radioactive sulphur ($S^{35}$) as sulfate.

Net productivity, respiration, and gross productivity for the 3.5-hour period were determined by measuring the oxygen concentration (Winkler method) at the beginning and the end of the experiment. After each small withdrawal of water for radioactivity determination the loss was replenished with an equal amount of sea water in order to avoid formation of an air space in the bottle.

In estimating surface-to-volume ratios, *Chondrus*, *Fucus*, *Sagrassum*, and *Ulva* were considered to be two-sided plates; hence, the surface-per-volume ratio is simply $2/t$ where $t$ is the average thickness of the blade. *Ceramium* and *Cladophora* were considered to be cylinders; hence, the surface-per-volume ratio is $2/r$ where $r$ is the average radius of the filaments. Since the middle half of *Chorda* is practically a cylinder and the quarter at each end tapers to a point, the surface-per-volume ratio of this cylinder-plus-two-cones is $9/4r$, where $r$ is radius of the cylinder and the base of the cones. These estimates do not take into account the additional areas of the edges and ends of these geometrical solids, nor irregularities such as "hairs," bladders, and vesicles, but for species and specimens used these features were relatively minor in so far as having a substantial effect on the ratio.

## RESULTS

As shown in Figure 1, uptake of tracer (as indicated by the decline in radioactivity of the water) followed a simple exponential pattern for the duration of the experiment. In two "light" bottles allowed to run for 12 and 24 hours, respectively, a constant percentage uptake per unit of time continued for at least 12 hours, after which the curve began to flatten slightly. When algae were removed from bottles after the 3.5 hours in $P^{32}$ solution, washed gently in running sea water, and placed in bottles containing sea water only, no radioactivity could be detected in the water after 2–3 hours. Thus, it was clear that no detectable "back diffusion" or exchange of $P^{32}$ occurred during the short period of the experiments. In other words, although phosphorus is undoubtedly being exchanged continually, the number of radioactive ions leaving the plant is very small because of the much greater number of non-radioactive ions already in or on the plant.

To compare the behavior of the algae, the slopes of the uptake curves were computed and the rate converted to per cent uptake per hour per gram dry weight of algae. In some of the experiments the uptake rate was higher or more irregular during the first half-hour than during subsequent periods (see *Ulva* curve, Fig. 1) suggesting an absorbtion reaction. Accordingly, rates during the first 1.5 hours and each of the subsequent two hours were used to determine the average for the experiment and to plot the

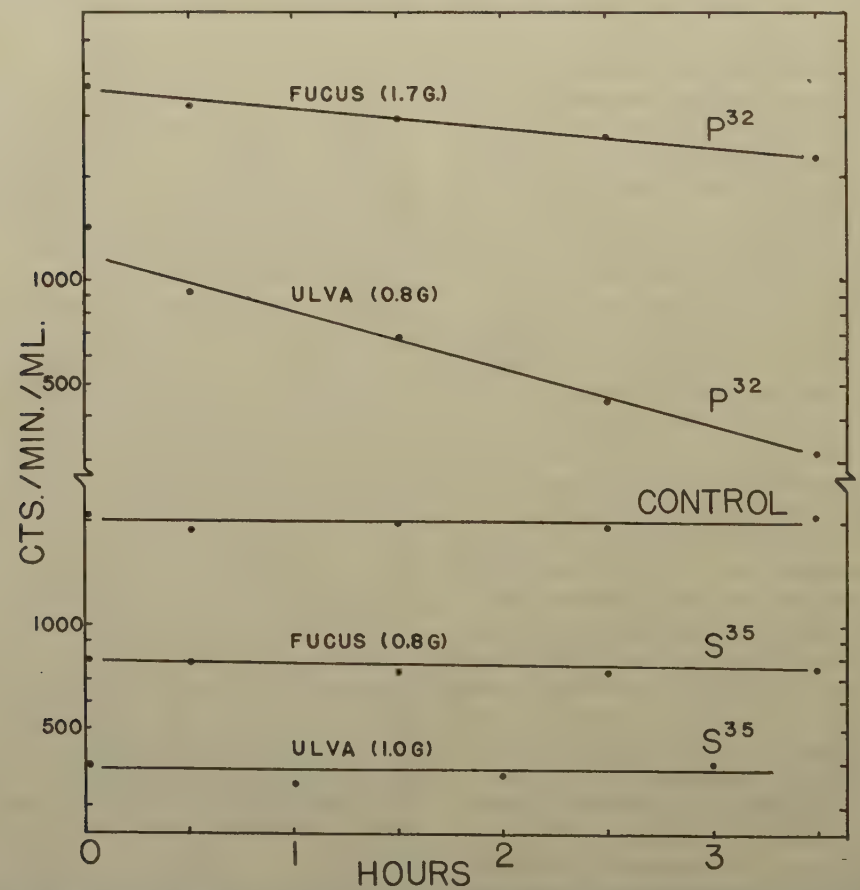


FIG. 1. Uptake as indicated by the decline in radioactivity of the media in four individual experiments and a control illustrating the method used in comparing species of algae and isotopes. In this graph the slopes of the $P^{32}$ curves have not been corrected for the differences in the amount of alga (dry wt. in parentheses) used. All experiments shown are "light" bottles.

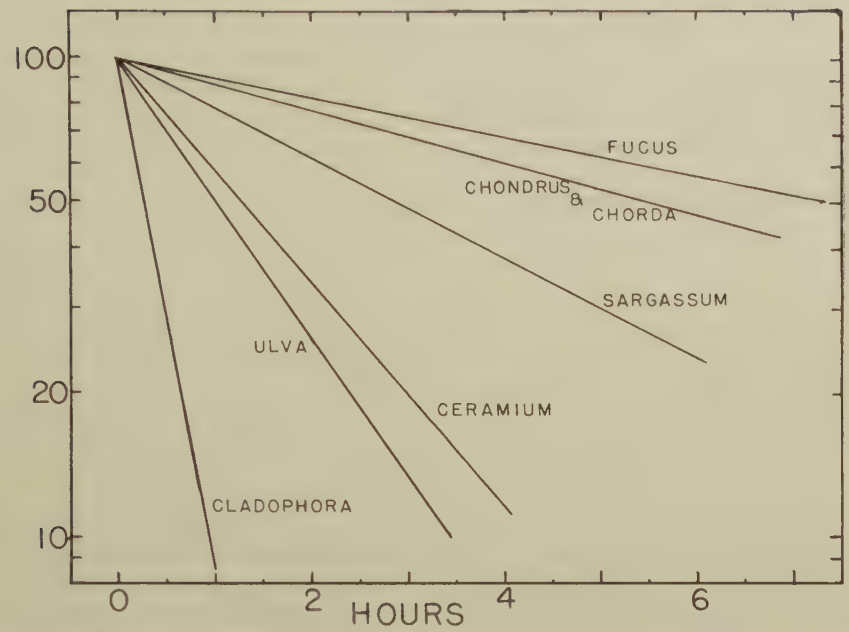


FIG. 2. Relative rate of uptake of $P^{32}$ in terms of per cent depletion of radioactivity in the water per gram of alga for seven species of benthic algae. The slope of each curve is the average of all experiments (including both "light" and "dark" bottles); in each experiment the rates of uptake during the intervals 0–1.5, 1.5–2.5, and 2.5–3.5 hours were averaged and corrected for small variation in the biomass of alga used.

TABLE 1. *Summary of paired light and dark bottle experiments measuring $P^{32}$ uptake and metabolism at 21°C and 450 ft-cand. illumination*

| Genus | Expt. No. | $P^{32}$ uptake %/g/hr | | Metabolism ml $O_2$/g/hr | | |
|---|---|---|---|---|---|---|
| | | Light | Dark | Net production | Respiration | Gross production |
| *Fucus* | 1 | 8.4 | 5.2 | 0.49 | 0.23 | 0.72 |
| | 2 | 11.3 | 6.5 | 0.64 | 0.22 | 0.86 |
| | 3 | 10.1 | 13.7 | 0.42 | 0.32 | 0.74 |
| | 4 | 12.6 | — | — | — | — |
| | 5 | 7.0 | 6.2 | — | — | — |
| *Chondrus* | 1 | 12.9 | 21.6 | 0.52 | 0.31 | 0.83 |
| | 2 | 5.4 | 7.0 | 0.82 | 0.30 | 1.12 |
| *Chorda* | 1 | 11.8 | 10.7 | 0.40 | 0.25 | 0.65 |
| *Sargassum* | 1 | 19.7 | 23.2 | 0.46 | 0.61 | 1.07 |
| *Ceramium* | 1 | 46.2 | 54.3 | 2.08 | 0.88 | 2.96 |
| | 2 | 33.8 | 30.3 | 3.36 | 0.68 | 4.04 |
| *Ulva* | 1 | 37.4 | 47.0 | 3.16 | 0.97 | 4.13 |
| | 2 | 52.6 | — | — | — | — |
| | 3 | 58.6 | — | 3.33 | 0.82 | 4.15 |
| *Cladophora* | 1 | 73.0 | 81.7 | 3.18 | 1.02 | 4.20 |
| | 2 | 108.9 | 100.6 | 5.30 | 1.50 | 6.80 |

TABLE 2. *Uptake of tracer $P^{32}$ by seven species of benthic algae in relation to gross production and surface/volume ratios*

| Species | Average rate $P^{32}$ uptake %/g/hr | "Ecological Half-life"* hours | Average gross production at 450 ft-cand. ml $O_2$/g/hr | Surface/volume ratio $cm^2/cm^3$ |
|---|---|---|---|---|
| *Fucus vesiculosis* | 9.1 | 7.3 | 0.77 | 33 |
| *Chorda filum* | 11.3 | 5.8 | 0.65 | 17 |
| *Chondrus crispus* | 11.8 | 5.5 | 0.97 | 20 |
| *Sargassum filipendula* | 21.4 | 2.9 | 1.07 | 200 |
| *Ceramium rubrum* | 41.1 | 1.3 | 3.45 | 100 |
| *Ulva lactuca* | 48.9 | 1.03 | 4.14 | 400 |
| *Cladophora glaucescens* | 91.0 | 0.3 | 5.50 | 670 |

* Number of hours required for one gram to remove one-half of radioactivity from the water. Since the absolute half-life values depend on the size of the bottle (constant in these experiments) these figures should be considered as relative only.

smoothed curves shown in Figure 2. The results of each of the experiments are shown in Table 1, and a comparison of species is summarized in Table 2 and in Figure 2.

The most striking feature of the results is that per cent uptake per hour per gram was similar in the light and in the dark for a given species but markedly different between species. Of the 13 paired experiments,

rates were somewhat higher in the light bottle in six and higher in the dark bottle in seven. Obviously during these first few hours most of the $P^{32}$ was entering what plant physiologists call the "outer space" of the plant, that is, adsorbing onto the surface or entering intercellular spaces or the cell sap. The light intensity in the experiment was low in terms of full sunlight; under less limiting light conditions, of course, the

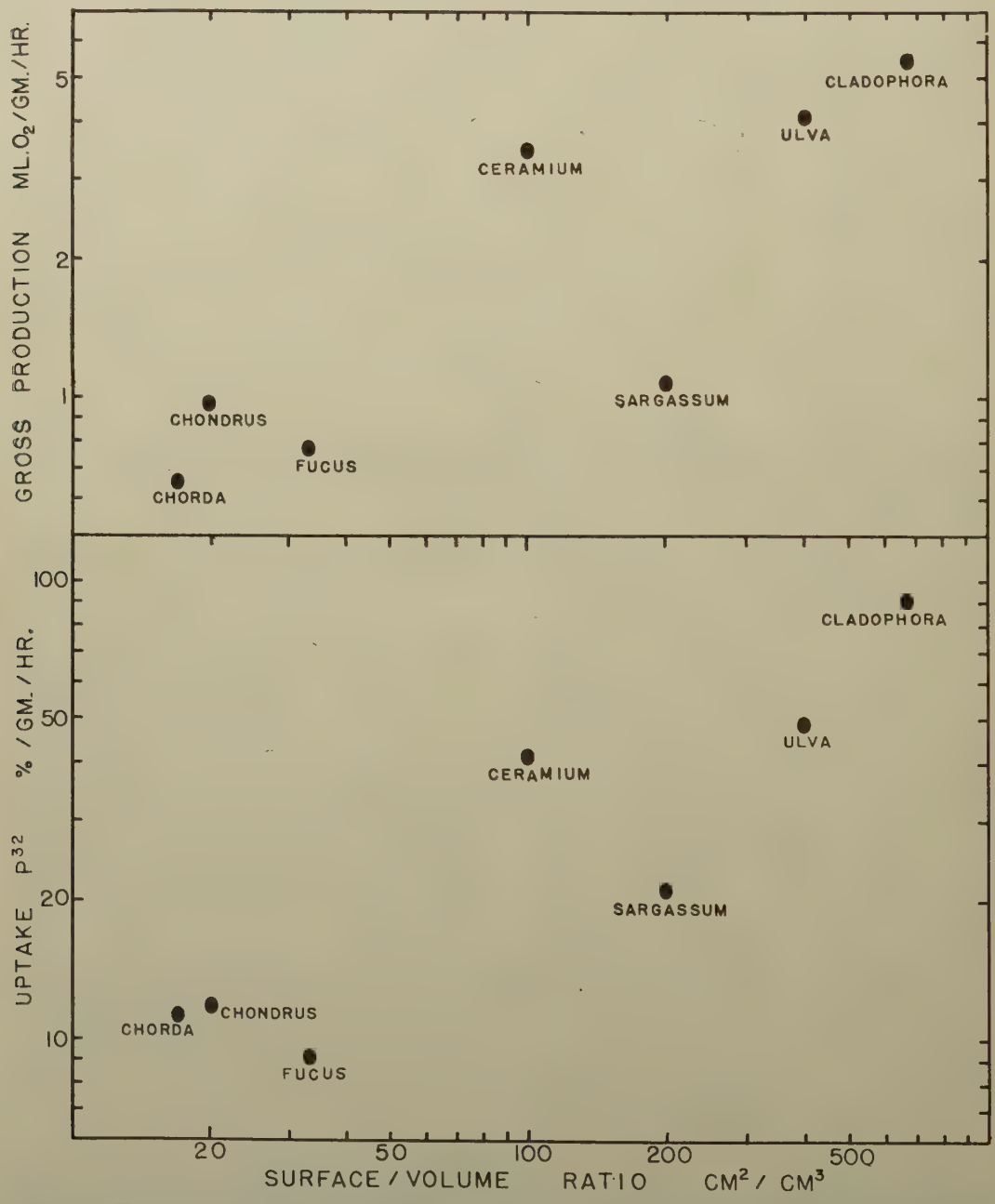


FIG. 3. $P^{32}$ uptake rate and gross production rate plotted against surface/volume ratio. Both rates are roughly proportional to surface area even though uptake of $P^{32}$ is not dependent on production.

uptake rate in the light bottle could exceed that in the dark. More interesting ecologically were the wide differences in the ability of a gram of the different species to "absorb" the tracer. The best way to visualize these differences is to consider the "ecological half-life" of the isotope in the water, that is, the time required for half of the radioactivity to disappear from the water due to both radioactive decay (slight for the short time involved) and uptake by the organism. As may be seen in Table 2 or in Figure 2 the time was computed to be 7.3 hours for *Fucus* and only 0.3 hours for *Cladophora* indicating that uptake per gram biomass was 25 times greater in the latter species.

Species exhibiting rapid uptake also had high surface-per-volume ratios and high production rates when supplied with light. As shown in Figure 3, both uptake and gross production rate appeared to be roughly proportional to the surface-per-volume ratio. These data suggest that tracer amounts of $P^{32}$ and, therefore, phosphorus in general are absorbed at a rate determined by the inherent structural surface area features of the alga. In other words, high surface-per-volume ratio increases the uptake rate as well as increases the ability of a given biomass of plant to fix energy under favorable conditions. Therefore, under these conditions uptake is related to potentional production rate and not to the metabolic level occurring at the time of measurement.

In a few experiments with *Fucus* and *Ulva* where $S^{35}$ was substituted for $P^{32}$ no uptake could be detected (see Fig. 1) even when one bottle was allowed to continue for 19 hours. Sulfate, in contrast to phosphate is abundant in sea water in terms of the requirements of the organisms. Since the concentration of sulfur in algae is only about ten times that in sea water, uptake, if any, during the short time period would likely be too small to detect by the methods used.

## DISCUSSION

Interpreting these results in the light of the results of mass applications of $P^{32}$ to lakes and other large systems (see Hutchinson 1957), an hypothesis suggests itself which might be tested by further experiments. It seems likely that the initial or short-term rate of tracer removal is largely dependent on the quantity of surfaces (both living and non-living) exposed to the environment. The more living surfaces of producer organisms there are, the more potentially productive the system should be. Therefore, the rate of tracer uptake might be a better index of what the system "can do" given favorable conditions of light, temperature, etc., rather than a measure of what it "is doing" at the moment, provided there is any sort of consistent relationship between these living surfaces and other sorptive surfaces.

Figure 3 is interesting in connection with size-metabolism relationships which are important in determining the biomass that can be supported with a given production rate. We see that intertidal macroscopic algae follow the same pattern as other organisms in that metabolism per gram decreases with increasing size of individual; critical size in this case is determined by the thickness or massiveness of the "branches" of the seaweed. Thus, given the same energy flow the standing crop of dry biomass of *Fucus* will be many times greater than that of *Cladophora*.

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## The Venice System for the Classification of Marine Waters According to Salinity

An international Symposium for the Classification of Brackish Waters, sponsored by the International Association of Limnology and the International Union of Biological Sciences, was held in Venice, 8–14 April 1958. From it derived the following statement on the classification of marine saline waters. The complete proceedings of the symposium are to be published soon, presumably as an IUBS colloquium.

At the final session of the Venice Symposium a revised classification of marine waters according to salinity was adopted and recommended for universal application. It is a somewhat modified Redeke-Välikangas system, with the addition of zones for higher salinities in order to include the whole salinity range found in the marine region.

The modification of the Redeke-Välikangas system (which was designed for the waters of northern Europe) is primarily confined to shifting the lower part of the mesohaline zone to the oligohaline zone in order to express ecological conditions encountered in southern Europe, South Africa, and some other areas. The term "brackish" as a classificatory term was avoided because of its ambiguous meaning, and the term "mixohaline" was proposed to indicate diluted sea water.

In order to express more adequately the conditions in such areas, for example as found in lagoons on the Mediterranean coast, the term "mixoeuhaline" was coined to include those coastal waters which have a salinity falling within the euhaline range but are at the same time of lower salinity than the adjacent sea.

For the sake of simplicity the various salinity zones have been defined by rather precise figures, but it was stressed that these figures are approximate, as indicated by the use of the ± sign.

The system adopted by the Symposium, with the approximate salinity ranges, is as follows:

| Zone | Salinity ‰ |
|---|---|
| Hyperhaline | >±40 |
| Euhaline | ±40–±30 |
| Mixohaline | (±40) ±30–±0.5 |
| Mixoeuhaline | >±30 but < adjacent euhaline sea |
| (Mixo-) polyhaline[1] | ±30–±18 |
| (Mixo-) mesohaline | ±18–±5 |
| (Mixo-) oligohaline | ±5–±0.5 |
| Limnetic (freshwater) | <±0.5 |

In view of the transitional character of the floral and faunal boundaries between zones within saline areas in nature, as well as their regional and local variation, any salinity classification can correspond only approximately with the zonation of the flora and fauna. It should also be remembered that reference given even to the best possible system will never give more than the average salinity conditions in a given water; additional details of the salinity range—both diurnal, seasonal, and annual, of the incidence of maxima and minima, and other highly varying features of paramount ecological importance—will always be necessary (cf. the halothermographs = hydroclimagraphs, by Hedgpeth 1951, in: Rep. Committee Treatise Mar. Ecol. Paleoecol. **11**).

In order to indicate waters of unstable or variable salinity (irrespective of mean values), the term "poikilohalinity" (adj. "poikilohaline"), in a sense slightly modified from that of Dahl (1956), could be used. The condition of stable or constant salinity could then be described as "homoiohalinity" (adj. "homoiohaline"). Explanatory terms of the type proposed by Rochford (1951, in: Austr. J. Mar. Freshw. Res., **2**) and R. Smith (1957, in: Ann. Biol., **33**, 1/2) might be useful. Subdivision of the adopted zones

[1] In this system the older and more familiar terms of the mixohaline series, polyhaline, etc., should be used in reference to the values of this system (the "Venice system"), and authors are requested to indicate that they are using this scheme in order to avoid misunderstanding.

covering more local conditions will also prove useful or necessary in many cases. As an example, in the Baltic Sea the following subdivisions of the meso- and oligohaline zones, based on biological observations, are important:

| Zone | Salinity ‰ |
|---|---|
| (Mixo-) mesohaline | |
| $\alpha$-mesohaline | ±18–±10 |
| $\beta$-mesohaline | ±10–±5 |
| (Mixo-) oligohaline | |
| $\alpha$-oligohaline | ±5–±3 |
| $\beta$-oligohaline | ±3–±0.5 |

In other cases, as, for example, the Australian estuaries with their extreme, climatically conditioned salinity oscillations which render any strict system inapplicable, reference to universally adopted terms for waters of different salinity may at least facilitate description of areas and characterization of the fluctuation range.

It was agreed that any attempt to classify inland saline waters would be premature in view of our incomplete and scattered information, and the hope was expressed that some standard way of expressing the salt content of such waters could be adopted or recommended by the International Association of Limnology.

## International Oceanographic Congress

The American Association for the Advancement of Science in cooperation with Unesco and the Special Committee on Oceanic Research of ICSU is planning and organizing an International Oceanographic Congress to be held during a two-week period from 30 August to 12 September 1959 at the United Nations Building, New York.

The purpose of the Congress is to provide a common meeting ground for all sciences concerned with the oceans and the organisms contained in them. The Congress will be devoted to the fundamentals of the marine sciences rather than to their applications.

It has been agreed by the organizing committee that the Congress will be centered around five symposia on the oceans:

1. The history
2. The boundaries
3. The deep sea
4. Dynamics of organic and inorganic substances
5. The marine life regime

1. *The history*—Includes discussions of the shape and structure of the ocean basins, the acting forces and processes, the origin of sea water and marine organisms, the stratigraphy of the deep sea and the climatic record.

2. *The boundaries*—Includes discussions of the coupling of sea and air, sea level, epicontinental sediments, estuarine and nearshore circulation (including the estuarine environment), influence of land masses on the behavior and distribution of marine organisms, and surface films and their importance in exchange processes.

3. *The deep sea*—Includes discussions of the geochemistry and physics of circulation, stirring and mixing in the ocean, nature and origin of bathypelagic life, distribution of pelagic sediment types (biological and physical interpretations), nuclear processes in pelagic sediments, and special characteristics of abyssal organisms.

4. *Dynamics of organic and inorganic substances*—Includes discussions of physical chemistry of sea water, biologically active substances in sea water, primary production, balance between living and dead organic matter in the oceans, exchanges between sea and air, exchanges between sediments and sea water, and vertical transport in the ocean.

5. *The marine life regime*—Includes discussions of the paleogeography of marine floras and faunas, biogeographical regions in the sea, evolution and adaptation in the sea, the behavior of marine organisms as influenced by environmental factors, physiology of marine plants, and the culture of

marine organisms as a means of understanding environmental influence on populations.

Each topic for a symposium will be considered for two consecutive days. Three invited lectures will be given each morning. The afternoon sessions will be organized around the morning topics, either in round-table discussions, in seminars, or in a series of papers. Several groups may run concurrently. Papers for the afternoon sessions will be selected from those received in response to this and subsequent announcements. Not all papers which have been accepted will actually be presented, but all accepted papers will be available at the meeting in mimeographed form. Titles and abstracts should be submitted as soon as possible and in no case later than 1 February 1959. The completed papers must be submitted by 1 May 1959 in order to allow time for duplication and distribution to the participants in the afternoon meetings well in advance of the meeting. All papers must have an abstract in a second language of the Congress. Papers may be presented in English, French, German, Russian, or Spanish. Simultaneous translations will be available for at least some of these languages.

The organizing committee expects that contemporary advances in the marine sciences, rather than reviews of older published work, will be presented under these broad topics. It is hoped that the younger staff members of the various oceanographic laboratories around the world will be encouraged to attend and to take part in the Congress. In order to assist with their attendance, the committee hopes to obtain funds to help defray the travel expenses of these younger participants. The committee also hopes to be able to contribute towards the travel expenses of the invited speakers at the morning sessions.

This notice should be considered as preliminary. Until further notices are issued, titles and abstracts of papers, which are publicly solicited by this notice, and any other correspondence should be sent to:

Dr. Mary Sears, Chairman
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts, U.S.A.

Other members of the Committee on Arrangements for the Congress are: Gustaf Arrhenius, John Cushing, Henry M. Stommel, Fritz Koczy, George S. Myers, Roger Revelle, Gordon Lill, Lionel A. Walford and Dael Wolfle (ex-officio).

# BOOK REVIEWS

GESSNER, F. 1957. **Meer und Strand.** 2nd Ed. VEB Deutscher Verlag der Wissenschaften, Berlin. 426 pp. DM 44.30 (= approx. U.S. $10.63)

The path of he who attempts to write a textbook on the science of the sea is beset with dangers, from the Scylla of producing a book of anecdotes about strange animals, to the Charybdis of devoting so much space to explaining currents, tides, and salinity that there is little room left for discussing the organisms subject to these environmental variables. Then there is the danger of concentrating too heavily on one part of the marine environment, let us say the shore, or of emphasizing unduly the purely descriptive aspects, or of trying to be too comprehensive or too detailed, and so on.

Perhaps the ideal textbook on marine science will never be written, since the various aspects and geographic areas of the sea, ranging from marsh to coral reefs, from the Arctic Sea to the Indian Ocean, pose so many different problems that to take account of all of them in a readable volume is impossible. However, one way of surmounting this difficulty might be to write a series of monographs on restricted parts of the sea and to attempt complete coverage of all the ecological and biological factors and facts by which this particular part of the sea is characterized. In this manner the subject would be represented by a series of books in which the multitude of phenomena would stand out like a mosaic against a background of common trends and ideas.

One of the best contributions towards such a future "library of marine science" is the new edition of Prof. Fritz Gessner's book. In fact, I consider it one of the most informative books on the sea that have appeared so far. The author gives an account of the history, hydrography, and biology of the North Sea and the Baltic, and by carefully apportioning the right amount of space to the various topics he achieves such a balanced representation as is rare to-day. One finds an intelligent and up to date discussion of the problem of productivity in the sea along with a descriptive account of animal and plant communities in various habitats. (I mention this particularly since the American reader is usually subject to discussions of *either* productivity problems *or* descriptive ecology, for which reason he is likely to forget that these two topics are but two sides of one and the same coin.)

Plant and animal communities are in the main treated with equal skill, although it should be pointed out that the chapter on the fauna of the Baltic shores is deficient in many respects, being based almost entirely on Remane's paper of 1933, while important contributions by Backlund (1945), Dahl (1946, 1948), Ax (1951), Gerlach (1953), etc., are totally neglected in both book and bibliography. It seems to me that it would have been more appropriate to take account of some of these papers rather than discuss the orientation of *Talitrus*, which was investigated by Pardi and Papi (1952–54) on material from the Mediterranean.

Some other deficiencies cannot be blamed upon the author, but show, rather, how incomplete is our knowledge of certain aspects of the marine environment. The fauna of sublittoral rocky bottoms, for example, is hardly explored, and consequently the relevant chapter in Gessner's book is more conspicuous for its omissions than for its contents.

Ecologically, the most important feature of the Baltic is, of course, the reduction in salinity from the Skagerrak via the Kattegat, the Arkona basin to the Finnish coast. In addition to the salinity gradient along the surface there is to be found a vertical stratification, with the North Sea water of higher salinity occupying the deeper zones and pushing southward and eastward into the basin of the Baltic. This situation, together with the effect of salinity on the organisms, is elucidated in an excellent chapter that is to be particularly recommended.

For the benefit of a future edition—which, it is to be hoped, will be prepared—it should be pointed out that despite the clear exposition of the principles of productivity the terms production and biomass are confused several times (*e.g.* on pp. 215, 257).

The illustrative material of the book is good, with the exception of the photographs taken in the Helgoland Aquarium. It is amazing how lifeless a living organism can look when not photographed by D. P. Wilson.

It can only be hoped that other authors will follow Gessner's lead and provide us with equally balanced accounts of other parts of the sea. How grateful one would be, for example, to have an exactly analogous representation of the Mediterranean, or, for that matter, of Puget Sound or the Gulf of Mexico. However, in order to set forth the history, hydrography, and biology of these areas with equal authority and clarity, much more effort will have to be put into studying even the more basic features such as the distribution and biology of important animals.

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VAN MEEL, LUDO. 1954. **Le Phytoplancton, état actuel de nos connaissances sur les grands lacs est-africains et leur phytoplancton.** Part A—Texte (681 pp), and Part B—Atlas (76 plates). Vol. IV, Fasc. 1, of "Exploration hydrobiologique du Lac Tanganika (1946–47)." Commission Administrative du Patrimoine de l'Institut Royal des Sciences Naturelles de Belgique. 31 Rue Vautier, Brussels, Belgium. Price 1250 Belgian francs (ca. U.S. $26.25).

It is not uncommon for foreign works to pass relatively unnoticed for sometime in our country. Van Meel's treatise on phytoplankton is one that deserves more attention by American workers.

From a standpoint of taxonomy alone this work is a fundamental contribution. Provided are records and illustrations for the nearly 900 species and 300 varieties of plankton algae from over 125 genera reported for eastern Africa. From the standpoint of the limnologist the assembled data and tabular data will make the work equally critical. It is a reference tool for future work on freshwater algae of Africa; but because of the large portion of species which are of world wide distribution, it also contributes a valuable reference for American algologists and limnologists.

The first volume consists of three distinct parts: a discussion of the general region and of its lakes; a systematic catalogue; and finally a presentation of limnological data and results of the investigation. The area covered is that along the African rift valleys in which lie the nineteen lakes studied. These extend from Lake Tana at the north in Ethiopia (ca. 12°N. Lat.), southward through Lake Rudolfe in Kenya, Lake Victoria which borders on Uganda and Tanganyika, Lake Tanganyika which borders on the Belgian Congo, Tanganyika, and Northern Rhodesia, southward to include Lake Nyasa (ca. 15°S. Lat.) which projects into Mozambique. This so-called East-African region is discussed in terms of its geology, hydrography, climatic factors, and general vegetation. The individual lakes are described and figured, although particular attention is drawn to Lake Tanganyika where the expedition's work was concentrated. Data and illustrations for this survey were drawn largely from the literature.

Data of especial interest to limnologists are to be found assembled in tabular form in the latter portion of the book. Included are values for dissolved oxygen concentrations, alkalinities, silicate, phosphate, and nitrate concentrations for certain of the lakes. The values are from samples taken at graded depths on indicated days. Van Meel's discussion clearly focuses attention on interesting relationships among the factors and plankton. A number of tables reveal distribution of algal species among the different lakes, among different stations in certain lakes, and in relation to certain factors. Breakdowns are also given for the proportions of different algal classes found at different stations and in different lakes.

A large portion of the main volume consists of the catalogue of species found. Names, synonyms, occurrence in the area, and plate number in the Atlas, are given for all entities listed; whereas additional descriptive data (in French) are provided where new information is being contributed. The comprehensive index to all epithets makes this catalogue especially useful.

The Atlas consists of a collection of illustrations taken from the published works of other specialists such as Hustedt, G. M. Smith, Schmidle, Woloszynska. Whereas no index is to be found in this volume, one can trace figures by means of the comprehensive index provided in Part A.

The works are both beautifully printed with large type and wide margins typical of the entire series. The size, 10 x 13 inches, is somewhat large by American shelf and reprint standards.

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BROWN, MARGARET E., *et al.* 1957. **The physiology of fishes.** Vol. I, xiii + 447 pp., $12.00; Vol. II, xi + 526 pp., $14.00. Academic Press, New York.

This is the first attempt made in English to gather together and integrate the large and diffuse body of existing information on the physiology of fishes. There is, therefore, a challenge here to each contributor to attempt a most careful appraisal of experimental methods, to sift and organize experimental data, to evaluate results critically, and to attempt to make significant generalizations. Naturally there is variation in the expertness and acumen with which different authors handle their material. Some of the articles in this compendium come close to meeting the high challenge. With one or two exceptions all are competent and thought-provoking reviews. All authors have not followed the editorial suggestion made in the preface to "indicate gaps in knowledge and lines of further research." This is disappointing, for a study of these papers brings into sharp focus the need for better coordination of research, and direction offered by experts in various fields could lead to significant advances in knowledge.

Papers are grouped in two general categories. Volume I bears the subtitle "Metabolism," and

Volume II is subtitled "Behavior," but as the editor points out "the terms are used in a broad sense since most chapters are concerned with both."

Articles in Volume I likely to attract the greatest number of readers are those on aquatic respiration, the cardiovascular system, digestion, excretion and osmoregulation, endocrine organs, reproduction, early development and hatching, and growth. A paper on air breathing discusses pertinent adaptations in those fish which are especially equipped for aerial respiration. Two other papers, "Skin and scales" and "Biochemical composition of fish," complete this volume.

Volume II will appeal particularly to students of physiological mechanisms of behavior. Articles of general interest include one on the nervous system, three on sense organs, three on behavior, and one on color changes. Likely to appeal to special interest groups are the contributions on the swimbladder, electric organs, luminous organs, and physiological genetics. Fish culturalists may be interested in the paper entitled "Water quality requirements of fishes and effects of toxic substances." An article dealing with the biochemical constitution and distribution of pigments in fish is also included in this volume.

Most of these reviews are comprehensive. Authors have been particularly careful to include information about cyclostomes, elasmobranchs, and teleosts. Inevitably, in a collection of papers on closely related subjects the problem of duplication of some material by two or more authors arises. This problem has been handled here with exceptional skill. There is a minimum of repetition, and a system of cross references to various discussions of the same material when they do occur is effectively employed.

Of inestimable value to all interested research workers is the careful documentation of source material by most authors. It frequently happens that an individual reference is cited by several authors; readers will be grateful that no attempt was made to save space by compiling a common reference list.

Also to be commended is the fact that detailed knowledge of anatomy of different kinds of fish is not taken for granted. Discussion of the physiology of each organ or organ system is preceded by an appropriate description of the anatomy of relevant structures.

In the opinion of this reviewer the most important single contribution is the paper on the nervous system. In this collection it assumes the central role as a reference work for most of the other papers, for it includes discussions of the nervous control of the different organ systems and of nervous coordination of behavior in the major groups of fishes. The excellence of this article is in keeping with its key position. It is an exhaustive and generally critical review of an extensive literature, full of exciting suggestions for further research.

Particularly outstanding among the contributions for their far-reaching scope, careful sifting of evidence, integration of information, critical and penetrating discussions and generalizations, and for their conciseness and clarity are those on the digestive system, the eye, and the acousticolateralis system.

Almost every paper will provoke ideas for further research in the minds of attentive readers. Especially stimulating in this respect are the articles dealing with the endocrine organs, gonads and reproduction, growth, conditioned responses, gustatory and olfactory senses, and aquatic respiration. On the debit side it may be remarked that in the discussion of endocrine organs the author assumes a rather more thorough knowledge of mammalian endocrinology than many of his readers may have, and that the article on conditioned responses takes for granted a familiarity with the concepts and terminology in this field which many readers may not possess. The paper dealing with the gustatory and olfactory senses is particularly stimulating because of the exciting implications of the fact recently demonstrated, that the chemical sense of fish is one of extraordinary sensitivity and range of discrimination. The author here attributes this acuity to the olfactory organs, although the experimental evidence for doing so is not clearly stated. However, the discovery that the chemical sense is so very acute brings it into an entirely new focus as a factor in the behavior of fish.

The editor is to be commended for including the two articles, "Ethological analysis of fish behavior" and "Reproductive and parental behavior." These two different approaches to the analysis of behavior provide stimulating and thought-provoking fare.

Somewhat disappointing are the papers dealing with the function of the swimbladder and with water quality requirements. The former is not so comprehensive as it could be and contains some inaccuracies. The latter offers a very superficial treatment of the physiological effects of water conditions.

Articles on pigments, on biochemical composition of fish, and on skin and scales do not deal with physiology and are out of place in these volumes.

A curious and deplorable omission from this collection, in view of the fundamental importance of the many and diverse effects of temperature, is a review of the state of knowledge about the temperature relations of fish and of any discussion of temperature perception and responses in fish. Also it may be noted, as a general criticism, that acclimation as a physiological phenomenon is not clearly taken into account and emphasized by most authors. This lack of attention to processes which are of such basic importance in the physiology of fish perhaps reflects the state of the science, for there is as yet insufficient recognition and appreciation of the significance of acclimation mechanisms, although they are likely to become

central problems for future researches in fish physiology.

Today, when the time required to ferret out and read original literature tends to be so great as to interfere with research, authoritative reviews are a necessity. A coordinated collection of reviews of knowledge about different areas of a field is indeed a boon to all workers in the field. In compiling these volumes the editor and contributors have done an invaluable service for all who are interested in fish physiology, not only because they have concentrated and made more accessible an immense amount of information but also because they have advanced the prospect for integration of this information.

These volumes will be of most use to people engaged in research in fish physiology, but many general physiologists engaged in work on other vertebrates will find them valuable as a reference in research and teaching, and may well discover in them many things to recommend fish as experimental animals for their researches.

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